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XXVII.

APHRODITE ACULEATA

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Liverpool Marine Biology Committee.

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ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

EDITED BY W. A. HERDMAN, C.B.E., F.R.S.,
AND JAMES JOHNSTONE, D.Sc.

XXVII.

APHRODITE ACULEATA

BY

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(With 10 Plates)

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EDITORS' PREFACE.

THE Liverpool Marine Biology Committee was constituted in 1885, with the object of investigating the Fauna and Flora of the Irish Sea.

The dredging, trawling, and other collecting expeditions organised by the Committee have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Thirty-six Annual Reports of the Committee and five volumes dealing with the " Fauna and Flora " have been issued. At an early stage of the investigations it became evident that a Biological Station or Laboratory on the seashore nearer the usual collecting grounds than Liverpool would be a material assistance in the work. Consequently the Committee, in 1887, established the Puffin Island Biological Station on the North Coast of Anglesey, and later on, in 1892, moved to the more commodious and accessible station at Port Erin in the centre of the rich collecting grounds at the south end of the Isle of Man. A larger Biological Station and Fish Hatchery, on a more convenient site at Port Erin, has since been erected, and was opened for work in July, 1902. In 1920 the Committee ceased to exist and the management of the station was transferred to the Oceanography Department of the University at Liverpool. The name " L.M.B.C. Memoirs " is, however, still retained.

In these thirty-six years' experience of a Biological Station, where University students and amateurs form a large proportion of the workers, the want has been frequently felt of a series of detailed descriptions of the structure of certain common typical animals and plants, chosen as representatives of their groups, and dealt with by specialists. The same want has probably been felt in other similar institutions and in many University laboratories.

The objects of the Committee and of the workers at the Biological Station were at first chiefly faunistic and speciographic. The work must necessarily be so when opening up a new district. Some of the workers have published papers on morphological points, or on embryology and observations on life-histories and habits; but the majority of the papers in the volumes on the "Fauna and Flora of Liverpool Bay" have been, as was intended from the first, occupied with the names and characteristics and distribution of the many different kinds of marine plants and animals in our district. And this faunistic work will still go on. It is far from finished, and the Committee hope in the future to add still further to the records of the Fauna and Flora. But the papers in the present series, started in 1899, are quite distinct from these previous publications in name, in treatment, and in purpose. They are called "L.M.B.C. Memoirs," each treats of one type, and they are issued separately as they are ready, and will be obtainable Memoir by Memoir as they appear. It is hoped that such a series of special studies, written by those who are thoroughly familiar with the forms of which they treat, will be found of value by students of Biology in laboratories and in Marine Stations, and will be welcomed by many others working privately at Marine Natural History.

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OCEANOGRAPHY DEPARTMENT,
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L.M.B.C. MEMOIRS

No. XXVII. APHRODITE ACULEATA

BY
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CONTENTS

PAGE
Introduction 1
Systematic Position 4
External Features 5
Integument 20
Anatomy of Internal Organs 28
Coelom and Coleomic Fluid 29
Circulatory System 31
Respiration 34
Digestive System 40
Musculature 58
Reproductive Organs 62
Nephridia 66
Nervous System 70
List of Literature 85
Reference Letters 89
Description of the Plates 91

INTRODUCTION.

THE polychaet worm, *Aphrodite aculeata* (Plate I), is commonly called the sea mouse. Its general characters have long been well known, a fact in which its remarkable beauty has probably played some part.

Linnæus (43) originally described the worm as *A. nitens*, but subsequently he (44) redescribed it as *A. aculeata*, a name which was also adopted by Baster (4). Linnaeus describes the fringe of setae, which clothe the body laterally, "as reflecting the sunbeams from the depth of the sea, exhibiting as vivid colour as the peacock itself, spreading its jewelled train." Cuvier (10) notes " des faisceaux de soies flexueuses brillantes de tout l'éclat de l'or et changeant en toutes les teintures de l'iris. Elles ne le cèdent en beauté ni au plumage de colibris ni à ce que les pierres précieuses ont le plus vif." In Gmelin's edition of Systema Naturae (45), Aphrodite is placed with Doris in the group Vermes Mollusca, though these forms have little in common except a general resemblance in shape. Swammerdam (64) described the worm under the name " Physalus " and, on account of its dorsal spines, he regarded it as being related to the sea urchins, though Rondelet (56) had previously classified it as a worm.

Pallas (48) redescribed Aphrodite and figured its general internal anatomy. He removed it from the Mollusca of Linnaeus and grouped it with Nereis and Serpula. Since this date many workers have added to our knowledge of this form. A resume of much of the literature on the animal is given by McIntosh (47).

The Sea Mouse is common off the coasts of the British Isles, France and the Baltic countries ; it is also to be found in the Mediterranean and the waters of North America. It is generally dredged from areas with muddy bottoms, in depths of from 20 to 25 metres, but it has also been reported from a depth of 580 metres. The northern species varies in length from one to six or seven inches and reaches three or four inches in breadth. Average-sized specimens from Plymouth and Naples vary between four and five inches in length. Sea mice are sometimes thrown on shore in great numbers. McIntosh mentions a storm in St. Andrews, in 1857, which left the coast strewn with multitudes. A similar but smaller species, *Aphrodite australis*, inhabits the Australian seas, maximum-sized specimens reach four inches in length.

The larval form, or trochosphere, is unknown. The dorsal spines in young specimens are relatively much longer than in the adult ; they meet in the middle line and protect the dorsum in the manner characteristic of Hermione. The movements of the sea mouse are rather slow. In aquaria, individuals often fail to exhibit any response to stimulation ; frequently they do not even right themselves if they are turned over on to their sides or backs. In coarse, shelly or gravelly deposits they rarely burrow, they merely lie on the surface, but in their natural finer grained element they may often be watched slowly burrowing head first into the mud, with a half screw-like motion of the body. The anterior feet are used to scoop away the mud which is heaped up laterally—the head end descends first and when burrowing is complete only the anal extremity remains uncovered.

The dorsal felt is dull coloured like the natural background. It serves as a sieve and protects the dorsal surface from clogging with mud. This part of the body wall has a respiratory function and it is illustrated by the fact that, if worms are put into water too shallow to cover them, they always lie on their backs. The felt and parapodia frequently serve for the attachment of foreign bodies. Hydroids commonly occur in bunches, hanging from the feet and the felting ; small bivalves are sometimes found attached in the same positions. The felt occasionally encloses small annelids and crustacea, though these latter are probably only incidental visitors. Frequently numbers of nematodes are found circulating beneath the felt.

All the Aphroditidae are carnivorous. According to Darboux (15) their normal diet consists of Diatoms, Amphipods, Isopods, Hydroids, Sponges and other smaller Annelids. The remains of small Molluscs and Holothurians have also been found in the alimentary tract.

SYSTEMATIC POSITION.

Aphrodite aculeata belongs to that group of the Polychaeta, the Phanerocephala, which includes Nereis, Polynoe, and many of the commonest marine worms.

The Phanerocephala are characterised by the possession of a prostomium which retains its ancestral position as a lobe overhanging the mouth. The prostomium bears, in addition to the eyes, sensory processes such as tentacles and palps. The trunk segments are all more or less similar.

The group is divided into eleven sub-orders, defined by the characters of the " head appendages " and the parapodia. The sea mouse belongs to the sub-order Nereidiformia, which includes many of the best known Polychaets, for example, Nereis, Syllis, Phyllodoce and Hermione. The members of this sub-order are characterised by the possession of well-developed tentacles and palps. The peristomium usually bears special cirri. The parapodia are well-developed locomotor organs supported by acicula and provided with dorsal and ventral cirri. The setae are usually jointed.

The eversible buccal region leads into a muscular pharynx armed with chitinous jaws.

Septa and nephridia occur regularly throughout the body.

The Nereidiformia contains thirteen families. It is only necessary to mention a few here, e.g. :—

Family Syllidae = Syllis.
,, Hesionidae = Hesione.
,, Nereidae = Nereis.
,, Aphroditidae = Aphrodite, Polynoe, Hermione, Sigalion.
,, Phyllodocidae = Phyllodoce.

The Aphroditidae are characterised by the possession of " scales " or elytra. The intestine bears paired lateral diverticula or caeca. The body is oval, oblong, or vermiform. The number of segments is variable.

The head, situated dorsally, bears one or three tentacles and one pair of palps. There are generally two pairs of eyes.

There are three chief sub-families of the Aphroditidae, named after their principal genera :—

I. Sigalioninae.
II. Hermioninae.
III. Polynoinae.

They differ from one another in the characters of the head appendages and the setae, and in number and disposition of the elytra.

The sub-family Hermioninae is briefly determined by the following characters :—The body is oval and depressed. The setae are all simple. The notopodial setae are prominent and are directed upwards and backwards to protect the elytra. Neuropodial setae are strong. The peristomium bears setigerous parapodia. The prostomium bears a single median tentacle and a pair of long palps. The facial tubercle (page 8) is always visible beneath the median tentacle. The jaws are represented by thickened muscular projections.

The genus Aphrodite includes those members of the Hermioninae which possess fifteen pairs of elytra concealed by a felting of hair-like setae arising from the notopodia. In *A. aculeata* the notopodial setae are brilliantly iridescent.

EXTERNAL CHARACTERS.

The general shape of the body of Aphrodite is roughly oval. It is bluntly pointed at the extremities and dorso-ventrally flattened. The anterior end is distinguished by a pair of large forwardly-projecting palps (Pl. II, fig. 3, and

Pl. IV, fig. 32, *Pp*), which, during life, are slightly pinkish in colour and very mobile. They arise from the head, which is very small and is hidden beneath the felt.

The anus is situated dorsally at the more pointed extremity of the animal (Pl. I, and Pl. IV, figs. 32 and 35, *An.*).

The true dorsal surface is concealed by the dorsal felt (Pl. I, fig. 2*a*, *F.*), a coarse mat of dun-coloured threads through which stiff, shiny brown spines project upwards and backwards. The tips of the dorsal spines are blunt and smooth, but the shafts are covered with adhering mud. The mobility of the spines is very much reduced by the surrounding felt. In this character they differ markedly from the spines of Hermione. When Hermione is touched, the groups of spines immediately spread fanwise over the dorsum and their sharply-pointed tips readily pierce one's skin.

In a dorsal view of Aphrodite the feet are hidden by the beautiful fringe of iridescent setae which project from the sides of the body.

The skin of the ventral surface* is tough and cream-coloured, it is roughened by the presence of numerous little papillae (Pl. III, fig. 14, *Pap.*). In living or freshly-killed specimens it is semi-transparent so that muscles and the nerve cord (Pl. I, fig. 2, *Nc.*) are readily distinguishable through it. The nerve cord occupies the mid-ventral line, and on account of its bright red colour (see p. 70), in fresh specimens, it forms a characteristic feature.

The body is divisible into three regions; the anterior and posterior extremities are, respectively, termed the Prostomium (Pl. II, fig. 3, *Pro.*) and the Pygidium; the intervening region constitutes the Trunk. This region is formed of a series of forty-three segments which are similar to one another in general characters, both externally (Pl. I, fig. 1*b*), and internally (Pl. IV, fig. 32).

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* See page 21.

The prostomium arises from the pre-oral region of the larva and the pygidium is developed from the larval periproct. The trunk is developed from the intervening area. The segments are differentiated from before backwards, so that the youngest ones are posterior. The pygidium is, from its origin, of the same age as the prostomium. The extremities are thus not homologous with the trunk segments.

1. The Prostomium (Pl. II, fig. 3, *Pro.*), or head, is a small spherical mass bounded by smooth iridescent cuticle. It lies dorsally at the anterior extremity of the body. It is invisible in a ventral view because the first trunk segment or peristomium projects forwards beneath it (Text-fig. 1, p. 9).

The prostomium is provided with three sensory processes. A small median process—termed the median or unpaired tentacle (Pl. II, fig. 3, *T.*)—arises from the anterior face of the head. It consists of a basal segment forming an elongated cup (*Kt.*) from which a terminal filament (*Kt.*) arises (Pl. II, fig. 4). The total length of the tentacle is approximately equal to the diameter of the head. It is very readily detached.

The paired palps (Pl. II, fig. 3, *Pp.*), already noticed, are prominent muscular sensory organs which arise from the posterior ventro-lateral regions of the head. They consist of a somewhat swollen basal segment and a much longer terminal conical segment projecting forwards and outwards. The surface is finely crenated and bears numerous minute projections (see page 25).

The single pair of eyes (Pl. II, fig. 3, *Eye*) lie dorsally at the sides of the median tentacle. They are round yellowish patches, differing little in colour from the prostomium and projecting very slightly from its surface.

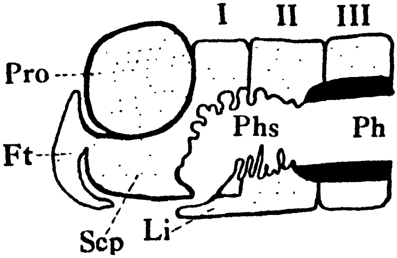
Sometimes two definite pigment spots are visible in each eye, but these are not always equally prominent and often appear to be entirely absent. The cuticle covering the surface of the eyes is very thin, but a thickened ridge is present round the rims.

A large papillated projection (Pl. II, fig. 3, *Ft.*), known as the facial tubercle, lies beneath the median tentacle and between the palps. This structure is present in the majority of the Aphroditidae, but its size varies considerably. It is especially prominent in many members of the genus Aphrodite. In the genus Polynoe it is absent. It is really part of the first body segment and will be described in the next section. Its function is sensory.

2. The Trunk. Each typical segment of the trunk bears two pairs of evaginations. Of these the most prominent pair, projecting laterally, are the parapodia (Pl. VIII, fig. 67, *Par.*), the organs of locomotion. The other pair are thin-walled pouches (*Tub.*) arising from the dorsal body wall; they thus lie in the cavity enclosed by the dorsal felt (Pl. V, fig. 38, *Tub.*), which must be removed to expose them. A median longitudinal incision in the felt at once brings the elytra into view. These leaf-like structures lie in a double row on the dorsum, which they completely conceal (Pl. I, fig. *2a, Eb.*). It is necessary to deflect the edges of the elytra in order to see the paired dorsal pouches, from some of which the elytra arise. The elytra-bearing pouches are distinguished as elytrophores, the non-elytrous ones are termed dorsal tubercles.

The two most anterior trunk segments are modified by the position of the prostomium and the mouth.

The mouth is a transverse slit in the ventral wall of the peristomium or first trunk segment. In Aphrodite the peristomium exhibits a marked difference from forms such as Nereis. The peristomium of Aphrodite bears parapodia and setae, whereas in Nereis and the majority of worms, this segment is devoid of feet and setae and only bears specialised cirri or sensory organs. The pre-oral portion of the peristomium projects forwards as a platform on which the prostomium rests (Text-fig. 1, *Scp.*). This structure is termed the sub-cephalic plate. It is characteristic of the Aphroditidae, but it is not equally prominent in all members of the group.



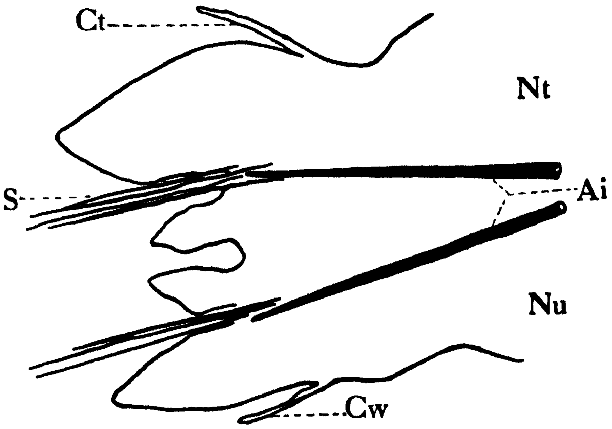
TEXT-FIG. 1. Diagrammatic median longitudinal section through anterior end of Aphrodite, to show the relationship of the prostomium to the peristomium.

That portion of the anterior extremity of the sub-cephalic plate which lies in the axial plane is drawn out to form the facial tubercle (Text-fig. 1, *Ft.*) already mentioned in the description of the dorsal view of the head. Its shape roughly resembles a cock's comb (Pl. II, fig. 5—lateral view). The dorsal edge (*d.e.*) is thickened and lies between the bases of the palps. The thin curved edge (*V.*) projects ventrally and posteriorly. The integument of the facial tubercle bears numerous sensory papillae (*Pap.*).

The aperture of the mouth is often concealed by a prominent muscular ridge termed the inferior lip (Pl. I, fig. 2, *Li.*). This structure is a forwardly directed transverse fold in the wall of the second trunk segment. It is marked by a series of longitudinal ridges which are obliterated when the lip is expanded by the protrusion of the pharynx. The integument of the angles of the mouth is thickened to form the lateral lips.

THE PARAPODIA.

Each parapodium (Text-fig. 2)—essentially a projection of the lateral wall of a segment—consists of a base and two rami. The dorsal ramus is termed the notopodium (*Nt.*) and the ventral one is known as the neuropodium (*Nu.*). In a generalised plan of a typical Polychaet parapodium, the two rami are approximately similar as, for example, in Nereis. The extremity of each ramus is invaginated to form a pouch (*Ss.*)—termed the setal sac—from which setae (*S.*) project. Each ramus is supported by an internal rod known as an aciculum (*Ai.*) and bears an external projecting filament termed a cirrus (*Ct.* and *Cw.*). Accessory flattened flanges are developed as swimming organs or for respiratory purposes. This generalised type of foot is characteristic of free swimming forms.



TEXT-FIG. 2. Parapodium of Nereis.

The parapodia of Aphrodite (Pl. II, figs. 6, 7, and 9) are somewhat specialised in a manner related to the mode of life. They are adapted to burrowing in mud and creeping on a soft bottom. The notopodia have the form of low rounded bosses. The neuropodia are the chief organs of locomotion, they project from the sides of the ventral surface as a paired series of little conical feet armed with short stiff setae. Aphrodite may be said to walk on its feet in much the same manner as a millipede. The motion is sinuous, groups of feet on the right and left sides are employed alternately.

In walking, the neuropodia are turned down ventrally, so that the setae stick into the mud and the central region of the body is slightly raised. The importance of the setae in progressing over a soft surface such as mud is at once demonstrated if a worm be watched whilst attempting to walk on a sheet of glass or any hard surface. The head is depressed so that the palpi and peristomial cirri may explore the path to be followed. As the anal extremity is always raised the parapodia of the posterior segments do not aid in progression, but their sensitive elongate notocirri (Pl. IV, fig. 35, *Ct.*) project upwards and wave freely in the water. The large anterior neuropodia serve as the chief burrowing organs.

The setae of the neuropodium are all short, stiff and brown in colour. They are arranged in three parallel transverse rows on the ventral aspect (Pl. I, fig. 1*b*). The most ventral (and proximal) row of setae are slender and numerous (from six to twelve bristles). The central row consists of from three to six stouter bristles. The dorsal (and distal) row contains two or three very stout setae with hastate tips. A short conical sensory filament—the neurocirrus (Pl. II, fig. 6, *Cw.*) projects outwards from the ventral wall of the foot.

The notopodia may be said to have lost all locomotory activity. They bear three types of setae, each of which serves a special purpose. Long filamentous setae form the dorsal felt which acts as a sieve to keep the dorsum free from muddy deposits. The stiff brown bristles are protective. When the worm rolls itself up rather like a wood louse, these spines form an effective armature. The third type of setae forms the iridescent fringe.

The setal sac of the notopodium is a depression occupying the dorso-lateral margin of the boss. The iridescent setae (Pl. II, fig. 6, *Si.*) issue from the ventral portion of the sac. The brown spines (*Sp.*), arranged in two groups, arise against the posterior wall of the depression. The dorsal group generally consists of five or six setae and the ventral group contains four, or more rarely, five. In both groups the setae have a fan-wise arrangement and project upwards and backwards through the dorsal felt (Pl. I, fig. 1*a*). A tuft of felting bristles, which is more conspicuous in non-elytrous segments, issues from the dorsal end of the setal sac (Pl. II, fig. 6, *Sf.*). Both felting and iridescent setae arise from the whole length of the anterior wall of the sac. In non-elytrous segments a sensory notocirrus (Pl. II, fig. 6, *Ct.*) arises from the posterior face of the notopodium between the two groups of brown spines. The notocirrus is much longer and more filamentous than the neurocirrus.

The parapodia of the first and second segments present some special points of difference from this typical foot. The parapodia of segment I (Pl. II, fig. 3, *Par.* I) are not markedly divided into dorsal and ventral rami. All the setae are iridescent, simple and hair-like, though somewhat stiff. They are grouped into three dense fan-like tufts. Both the notocirrus (*Ct.*) and the neurocirrus (*Cw.*) are filamentous; they arise close together from the posterior aspect of the foot.

The parapodia of the second segment (Pl. II, fig. 7) differ both in the type and the arrangement of the setae. The ventral (or proximal) row of bristles of the neuropodium form a dense group of short stiff setae armed with a double row of alternately arranged spines (*Sv.*). Similar toothed setae occur on the posterior feet (Pl. II, fig. 9, *S.*). The iridescent setae of the notopodium

(Pl. II, fig. 7, *Si.*) are stiff and form a dense fan issuing from the whole length of the setal sac. The felting bristles (*Sf.*) issue from the dorsal end of the sac. Setae comparable to the brown spines are represented by a few pale yellow bristles. The neurocirrus (*Cw.*) is elongate; there is no notocirrus, as the second trunk segment is elytra-bearing.

Setae.

The setae exhibit many interesting characteristics. Each seta is developed from a single cell situated at the base of the setal sac. Young neuropodial setae (Pl. II, fig. 8) can be examined from the base of the neuropodial setal sac. They are triangular in shape; the apices are armed with fine projections or spines. The sacs of the larger setae are situated well within the cavity of the parapodium so that the total length of a seta is considerably greater than the externally projecting portion (Pl. VIII fig. 70, *S.*).

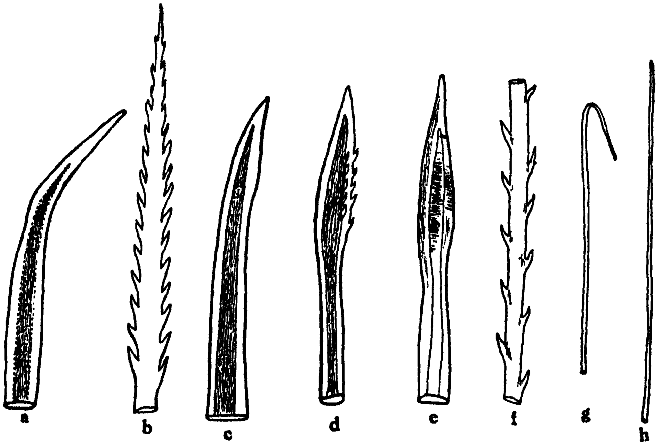
The stiff brown spines of the notopodium (Pl. II, fig. 6, *Sp.*) have a smooth shiny surface. Their tips are curved and slightly flattened.

The iridescent setae (Text-fig. 3, *h*) are long, thin, unjointed hair-like structures with pointed tips. The bristles of the dorsal felt are comparable to the constituent fibres of a typical seta (Eisig, 18) and not to the whole structure. They are long and flexible—their tips are curved (Text-fig. 3, *g*). They are slightly finer than the iridescent setae.

The majority of the neuropodial setae resemble the dorsal spines. They are stiff and smooth-surfaced. Their tips are flattened and slightly curved. In the Text-fig. (*a*) illustrates the form of the tip of setae from the ventral (or proximal) row, (*c*) is derived from the middle series, and (*e*) is a seta from the dorsal row.

Posterior to segment XXXIII the neuropodial setae are armed with tooth-like projections, the occurrence of which exhibits an interesting serial arrangement.

The setae of the middle row of neuropodium XXXIII terminate in spear-shaped heads bearing a double row of spines (*d*). On the feet posterior to this these setae become relatively longer and the spinous portion occupies progressively more of the total length until, on the most posterior feet, the spined tips are as long as the unspined shafts.



TEXT-FIG. 3.

In the dorsal row, spines are first encountered on neuropodium XXXV, posterior to which they vary in a similar manner.

The setae of the ventral (or proximal) row are both more slender and more numerous than those just described. Their tips are distinctly curved (*a*) ; posterior to segment XXIX they are spear-shaped (*c*). From segment XXX to XXXIV the tips are armed with a double row of spines. The setae of segments posterior to XXXIV are spined for almost their whole length (*f*).

The parapodia of the last six segments are very small (Pl. I, fig. 1*b*) ; the setae are few in number and are not arranged in definite rows (Pl. II, fig. 9, *S.*). Many are spined along their whole length.

Cirri.

There are two types of cirri. One consists only of a short sensory filament—the cirrostyle—which arises directly from the body wall (Pl. II, fig. 9, *Cw.*). In the other type the filamentous cirrostyle (Pl. III, fig. 10, *Ncs.*) arises from a basal evagination of the body wall, termed the cirrophore (*Ncc.*).

All the neuropodial cirri, except those of the first two pairs of parapodia, consist of a short cirrostyle. On the other hand all the notopodial cirri and the neuropodial cirri of segments I and II are provided with a basal cirrophore, and the terminal cirrostyle is long and filamentous. The cirri of the first segment are greatly elongated ; they are distinguished as the peristomial cirri. Notocirri are absent from all elytra-bearing segments. The notocirri of all segments posterior to the last pair of elytra are very long and have club-shaped tips (Pl. II, fig. 9, *Ct.*).

Elytra.

The fifteen pairs of elytra are borne on approximately alternate segments of the trunk (Pl. IV, fig. 32). They are essentially leaf-like epidermal expansions arising from the dorsal wall of the elytrophores. The elytra of the anterior segments are circular in shape, but the posterior ones are elongated towards the anus and are roughly triangular. The area of attachment of each elytron (Text-fig. 14, *A.*, p. 73) is a narrow ellipse, the long axis of which is placed at right-angles to the body axis.

The elytra completely cover the dorsal surface. They overlap one another from before, backwards, and individually from left to right and right to left, alternately. The marked patchiness of the exposed areas (Pl. IV, figs 30 and 32, *Ex.*) is due to a superficial encrustation; the elytra themselves are entirely free from pigment. Sometimes preserved specimens show elytra distended with fluid, but this is an unnatural condition and is due to the formation of a cavity into which fluids have penetrated.

The actual distribution of the elytra is as follows. The anterior pair arise from the elytrophores of segment II. Segment III is non-elytra-bearing. The second pair arise from segment IV and the following eleven pairs occur on all the odd segments from V to XXV inclusive. Segments XXVI and XXVII are non-elytrous. The last two pairs are borne respectively on segments XXVIII and XXXI. All elytrous segments are devoid of notocirri.

The dorsal tubercles bear little irregular projections termed dorsal fimbriated papillae (Pl. II, fig. 6, *Dtp.*); these structures, therefore, alternate with the elytra and are borne on the same segments as the notocirri. They are really folds in the integuments of the dorsal tubercles. The dorsal surface of the first body segment is reduced to a narrow transverse ridge and is devoid of any projections (Pl. II, fig. 3); the second body segment bears the first pair of elytra (*Eb.* 1), so the first pair of dorsal fimbriated papillae are represented by mere ridges with entire margins on segment III, and those posterior to the twenty-second segment are similar in shape. The dorsal fimbriated papillae occurring between these two limits are much larger, their edges bear numerous conical projections (Pl. III, fig. 11 *a*, *b*). The function of these organs is unknown; they have been variously interpreted as branchiae, rudimentary elytra and lymph glands. The ectoderm appears to lack the papillae numerous over the integument elsewhere. A marked thickening of the epidermis and a considerable development of gland cells (Pl. III, fig. 18, *Gc.*) greatly reduces the internal cavity, so that a respiratory function seems improbable.

Elytra are peculiar to and characteristic of the whole group Aphroditidae. The structure, function and homology of these organs have been the subject of much discussion. It is only in the genus Aphrodite and in one species of the genus Laetmatonice that they are concealed beneath a dorsal felt; in all other genera they form a striking external feature. Their mode of attachment to the elytrophore varies greatly in the different groups. In many genera the "scales" are readily cast off when the worm is irritated, as, for example, in Polynoe. The opposite condition is exhibited by Iphione, whose elytra are so firmly attached that they form a protective armour somewhat resembling the dorsal plates of Chiton. The capacity to throw off the scales is brought about by a formation similar to the intra-epidermal pocket of the notocirri (see p. 24) by which the area of attachment is reduced to a peripheral ring. The caducous scales characteristic of Polynoe are linked by a series of genera to the firmly-fixed enclosed condition of the elytra of Aphrodite. For example, *Hermione hystrix* often closely resembles a felted form. This is due to a fan-like group of stiff setae which lies flattened against each elytron and projects backwards and inwards towards the middle line (Pl. IV, fig. 36, *S.*). Numerous foreign bodies, such as hydroids and algae, become entangled in these setae and form a mat which conceals and protects the dorsal surface.

The functions of the elytra are various. They are always sensitive. In many forms they serve as organs for the production of phosphorescent light, as in *Polynoe elegans* and in some species of Harmothoë. Their protective value varies greatly in different groups. In some genera they are small and do not entirely cover the dorsum. In forms, such as many Polynoids, in which the scales are readily cast off, they are also rapidly reproduced. It is recorded that Harmothoë exhibits small new scales six weeks after the old ones have been shed.

The elytra often serve as roofs for incubating chambers. The connection of the elytra with the function of respiration (see p. 35) has long been recognised. The scales were once believed to be actual respiratory organs, but this view was entirely overthrown when their detailed structure was investigated. They are flattened epidermal expansions devoid of an internal cavity. They serve, by continual movement, to ensure the circulation of fluid over the respiratory surface (that is, the thin integument of the dorsum).

From a study of the habits of Annelids, Georges Bohn (6) has developed the following interesting theory relating to the elytra-bearing worms. He regards the natural habit of the primitive forms as parasitic or commensal. Living in the tubes of other Annelids the visitors are confined in a space occupied by a toxic medium. Progression and respiration become modified to fit in with this special environment. The movements of the Aphroditidae, both locomotory and respiratory, resemble those of the Nereidae and the Phyllodocidae. Life in a confined space led to the localisation of these two types of movement in different parts of the body. The ventral surface became a creeping sole for adhering to the inner wall of the host tube. Respiratory activity necessarily increased by reason of the toxic nature of the environment. Undulatory movements became confined to the dorsum, on which the elytra develop in response to mechanical and chemical stimuli. Bohn regards the free-living Aphroditidae as being secondarily developed from tube-inhabiting forms. To this history he traces their choice of a muddy habitat, deposits in which a certain amount of dead animal matter is necessarily included. The same history serves to correlate the helicoidal attitude often assumed by Aphrodite and its allies, with the spiral attitude characteristic of tube-living forms.

Homology of the Elytra.

The fact that the elytra alternate with the notocirri has led to the general view that the two structures are homologous (Beddard 5), the former being merely flattened cirrostyles, and this is supported by the similarity in mode of attachment of the two organs. Much discussion has taken place on this question. Darboux (13) regards the elytra and cirrostyles as two separate sets of structures which are mutually exclusive. He considers that the dorsal fimbriated papillae probably represent degenerate elytra. Later, Hans Duncker (16) refuted Darboux's ideas. He surveyed the whole of the elytra-bearing worms and finally re-established the homology of the elytra and cirri. In the case of Aphrodite, Duncker considers that the cirrostyle corresponds with the elytron and that the cirrophore and the organ of Darboux, together, correspond to the elytrophore. His view is supported both by topographical relationships and histological structure and also by the similarity of the innervation of the cirrostyle and the elytron. He disagrees with Darboux's topographical distinctions.

EXTERNAL APERTURES OF THE TRUNK.

I. The mouth has already been described (p. 8).

II. Nephridial apertures. The paired segmental organs, open to the exterior at the tips of small rounded papillae (Pl. III, fig. 12), situated on the posterior aspect of the parapodia at the bases of the dorsal rami. They thus lie in the grooves between the feet and are best seen from the dorsal surface, by cutting through the felt between successive segments, so that the parapodia may be drawn apart. The apertures of the papillae are directed dorsally. Typically there are fifteen pairs of papillae borne on segments XI to XXV, inclusive, but the number and position are subject to slight variation.

The genital products reach the exterior through these apertures.

III. Anus. This aperture is a slit in the dorsal wall. The integument surrounding it is infolded and plicate, and forms a structure termed the anal rosette (Pl. I, fig. 2*a*). There are no special anal appendages or urites, but the parapodia of the posterior segments bear elongated notocirri which form a highly sensitive fringe round the anus. It is further protected by the notopodial setae (Pl. IV, fig. 35).

THE INTEGUMENT.

The body wall consists essentially of a single layer of cells—the epidermis. It rests on a basement membrane and is covered on its free surface by a cuticle. Its structure is very varied in relation to its functions, the chief of which are concerned with protection, sensation and respiration.

The cuticle is an effective protective layer secreted by the epidermis, it is greatly thickened in special regions, such as on the surface of the prostomium, and on the ventral surface. As is usual in Annelids, the cuticle is built up of two series of fine fibres which intersect one another at right angles (Pl. III, fig. 13). This structure causes the characteristic brilliant iridescence of the surface. In sections it exhibits a fine stratification, the inner layers of which stain less deeply than the outer ones.

In general, the whole exposed surface of the worm is capable of receiving sensory stimuli, but special organs of sense are abundant and their form is very varied. Everywhere the skin is raised into little papillae. The largest and most readily seen are those on the ventral surface and on the neuropodia where their presence makes the skin feel distinctly rough. These papillae (Pl. III, fig. 14, *Pap.*) are spherical in shape and often dark-brown in colour. On the neuropodia they are arranged in rings so that the feet have an annulated appearance. The papillae on the dorsal surface are somewhat larger and are conical in shape (Pl. III, fig. 15, *Pap.*), whilst many of the other sensory structures are so minute as to be visible only under high magnification.

The integument of the dorsum is thin and colourless. The ventral integument is much thicker and often yellowish in colour. During life the whole surface is transparent, but this property is more pronounced dorsally than ventrally.

The epidermis consists of epithelial cells of two types—supporting cells and gland cells. The supporting cells (Pl. III, fig. 16) are cylindrical or somewhat " hour-glass " shaped. The basal ends of the cells are often ill-defined, they break up into fibre-like processes which pass into the basement membrane (Pl. III, fig. 17, *So.*). The nuclei are oval and are placed near the cuticular border. The gland cells (Pl. III, figs. 17 and 18, *Gc.*) occur between these supporting cells, they are rounded or elongate and communicate with the exterior by little canals which pierce the cuticle. Their nuclei are generally situated towards the base.

The epidermis of the dorsal fimbriated papillae (Pl. III, figs. 18 and 19) is an example of the more glandular type. The supporting cells are so greatly elongated that they may be said to form a scaffold in the spaces of which the gland cells are situated. The bases of the supporting cells pass into fibres which are interwoven with scattered sub-epidermal cells.

On the other hand the cells of the ventral body wall form a simple columnar epithelium (Pl. III, fig. 20) with very few gland cells. Between these two conditions of the epidermis there are many variations which will be treated in the descriptions of the special organs which they form.

The basement membrane is an important supporting tissue on which the epidermal cells rest, and to which the muscles are attached. It exhibits two chief varieties of structure, one of which is confined to the ventral body wall only and the other occurs everywhere else. The latter (Pl. III, fig. 21, *Bm.*) consists of a clear matrix containing a meshwork of very fine fibres. In preparations treated with Mallory's connective tissue stain, the matrix stains pale blue and the fibres exhibit a deeper tint—the whole layer forms a definite blue band, in sharp contrast to the red colour of the epidermal cells between the bases of which it projects. In the adult no nuclei are demonstrable in it. If, as Darboux (15) suggests, this layer is formed entirely of processes of the epidermal cells, these fibres suggest a special secretion.* In Mallory preparations it is rarely possible to trace the course of the epidermal cell processes for any distance into the basement membrane. The epidermal fibres are intermingled with nerve fibres. (The basement membrane supporting the epithelium of the alimentary canal is similar to this variety.) The second variety (Pl. III, fig. 22, *Bm.*), characteristic of the ventral body wall, is a typical connective tissue. In parts it reaches considerable thickness as, for example, at the bases of the neuropodia where so many muscles are attached, and beneath the ventral nerve cord. It consists of a clear matrix traversed by a very fine openmeshed network of fibres and containing scattered groups of connective tissue corpuscles.

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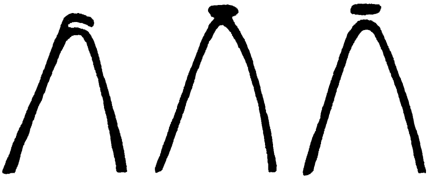
* See Footnote, page 28.

The spherical papillae of the ventral body wall are special areas where the cuticle is thin and the epidermal cells are, therefore, in close contact with the outside world. Each papilla (Pl. III, fig. 21, *Pap.*) is a little bulge of epidermal cells connected with the epidermis by a short stalk. The cells of the papilla are elongated, their expanded cuticular borders secrete a very thin cuticle and their basal ends are produced into long fibre-like processes which enter into relationship with fibres from the sub-epidermal nerve net and scattered ganglion cells (Pl. III, fig. 21, *Gs.*).

The conical papillae of the dorsal body wall (Pl. III, fig. 23) are groups of elongated cells covered by cuticle which does not vary in thickness from that of the intervening areas. The tips of the papillae bear little flattened caps attached at one side beneath which, however, the cuticle is not perforated (Text-fig. 4). These papillae, in addition to their sensory function, are probably a means of increasing the area over which respiration takes place.



TEXT-FIG. 4. Structure of cuticular caps of the papillae of the dorsal body wall.

With the notable exception of the palps all the external structures—elytra, facial tubercle, tentacle, sensory papillae, cirri, etc.—are essentially ectodermal folds. No muscles are involved, the mass is made up by a great development of connective tissue. For example, the facial tubercle (Pl. II, fig. 5) is essentially an expansion of epidermis surrounding a core of connective tissue. Its surface bears numerous sensory papillae (*Pap.*) like those of the ventral body wall. The papillae are innervated by branches of a nerve network lying at the base of the epithelium. The structure of the ridges of the inferior lip (Pl. III, fig. 22) is similar; the connective tissue (*Bm.*) which occupies the core of the folds is very elastic.

In contra-distinction to this type of folding which encloses a mass of connective tissue, the cirri consist entirely of epidermal cells. The median tentacle, the peristomial cirri and all the notocirri are similar in structure. Each consists of two portions, a basal segment or cirrophore (Pl. III, figs. 10 and 24, *Ncc.*), which is an evagination of the body wall and contains a diverticulum of the coelom (*Bc.*), and a sensory filament—or cirrostyle (*Ncs.*). The cirrostyle is a finger-like projection of the epidermis only, it arises from a little pit formed by the invagination of the tip of the cirrophore and its axis is occupied by a nerve (*N.*). The corresponding segments of the median tentacle are termed the ceratophore and the ceratostyle (Pl. II, fig. 4, *Kf.*, *Kt.*).

At the base of the cirrostyle the epidermis gives rise to a hollow mass of cells which projects into the cavity of the cirrophore (Pl. III, figs. 10 and 24, *Ip.*). This secondary cavity, to which the cirrostyle forms a " cap," is termed the intra-epidermal pocket; its development reduces the attachment area of the cirrostyle to a thin circumferential ring. On stimulation of the cirri the gland cells forming the walls of the pocket secrete mucus into its lumen and cause an expansion which bursts off the " cap." In this manner the shedding of the cirrostyles is readily brought about. A similar arrangement occurs in caducous elytra.

The cuticle of the cirrostyle (Pl. III, fig. 24, *C.*) is very thin; it is pierced by little canals through which minute processes of epidermal cells pass to the exterior and give rise to numerous hair-like sense organs (Pl. III, fig. 25, *Pap.*). The bases of the epidermal cells which form the papillae project as fine processes and intermingle with the fibres of the axial nerve and with scattered sub-epidermal fibre-cells. Similar but larger sense organs occur on the surface of the palps (Pl. III, fig. 26). These special groups of cells serve to bring the outside world into contact with the axial nerve. The course of the cirrus nerve is entirely intra-epidermal. The nerve of the notocirrus (Pl. III, fig. 24, *N.*) runs in the wall of the cirrophore to the base of the intra-epidermal pocket which it traverses obliquely till it reaches the axis of the cirrostyle. The structure of the neurocirrus is similar to that of the style of the notocirrus.

A comparison of the palps and cirri yields points both of similarity and contrast. The palps are essentially evaginations of the whole wall of the prostomium. They arise from its postero-lateral borders. At their bases they contain a cavity which is a diverticulum of the prostomial coelom, but distally they are solid. The nerve is eccentric and occupies the median dorsal line of the epidermis of each palp (Pl. X, fig. 82, *PpN.*). The cuticle is thick and iridescent, its free surface is finely crenated and bears minute hair-like projections (Pl. III, fig. 26). The epidermis at the base of the palp consists of elongated cells interspersed with gland cells (Pl. III, fig. 17) ; distally the gland cells are less numerous and the layer becomes a simple columnar epithelium (Pl. IV, fig. 27, *Ce.*). The basal processes of the epidermal cells are embedded in a layer of tissue formed of very fine circularly running fibres (*Ff.*) which, on treatment with either haematoxylin or Mallory's connective tissue stain, exhibit the same staining properties as the epidermal cells themselves. Et. Jourdan (37) termed this tissue " the circular muscle layer," and described it as resting on a thin hyaline membrane. This latter is the basement membrane (*Bm.*), as is clearly demonstrated by a deep blue colour in Mallory preparations. Darboux (15), in criticising this description by Jourdan, denies the actuality of the circular muscle layer on account of its situation between the epidermis and basement membrane. He explains its appearance as due to a dissociation of fibres of the basement membrane. This explanation seems unlikely, as the staining properties of the two tissues are clearly distinct. It probably consists of nerve fibres intermingled with the bases of epidermal cells and with sub-epidermal fibre cells, from its situation between the epidermis and basement membrane. Whatever its constitution it is certainly distinct from the basement membrane.

The epidermal tissues enclose a cylinder of muscles consisting of a number of separate bundles of longitudinal fibres (Pl. IV, fig. 27, *Lm.*) interspersed with a meshy tissue which occupies all the remaining space. This tissue is made up of fibre-like cells (*Fc.*) containing an oval nucleus in a very much reduced cell body. Many of the cells stretch from the basement membrane to the axis of the palp, where they form a dense network (Pl. IX, fig. 76, *Pp*).

The sensory papillae of the palp (Pl. III, fig. 26) have been compared by Jourdan to the sense hairs of the Insecta. They consist of little elongated groups of epidermal cells which project to the exterior through canals in the cuticle. The cuticular secretion of these projecting cells is so thin that they may be regarded as being in actual contact with the external medium. At the base of these papillae, process of the epidermal cells enter into relation with nerve fibres—ganglion cells are often present (*Gs.*). Sometimes the epidermal cell processes can be traced through the basement membrane to the fibre-cells (*Pns.*).

The elytra are flattened expansions of the epidermis. Much of their structure can be made out from whole mounts stained with haematoxylin. Figure 28 (Pl. IV) illustrates a portion of the edge of an elytron seen from the dorsal surface. The margin bears a row (sometimes several) of tiny " warts " (*Wt.*) which are present only on the dorsal surface. These structures are solid cones of cuticle.

In an examination of optical sections from the upper to the lower surface of an elytron, the following layers may be distinguished. The cuticle is unmarked by any excrescences except for the peripheral warts just mentioned. The nature of the brownish patches has already been described, they are foreign particles attached to the roughened surface of the cuticle (Pl. IV, fig. 30, *Ex.*).

The epidermis consists of flat polygonal squames, the boundaries of which are roughly indicated by clear lines (Pl. IV, fig. 28), their oval nuclei (*Nc.*) lie just beneath the cuticle. On focussing half way through the thickness of the elytron, scattered spherical nuclei (*Ni.*) and also the main nerve network (Text-fig. 14, p. 73, and Pl. IV, fig. 28, *N.*) are brought into view. Beneath this level the epithelium of the ventral surface is met with. The upper and lower surfaces of the elytron are connected by a series of fibres (Pl. IV, figs. 29 and 30, *Ef.*) which actually pass through the epidermal cells and are inserted into the cuticle (Pl. IV, fig. 28, *Ef.*). These fibres are clear and hyaline, each is rod-shaped with expanded ends. At the periphery of the elytron the fibres are regular and parallel (fig. 29), but in the central region (fig. 30) they are less evenly arranged and many do not join both cuticular surfaces. The interstices between the fibres are occupied by a finely granular protoplasm enclosing large vacuoles— and the scattered spherical nuclei already noticed (*Ni.*). The disposition of these nuclei is clearly seen in horizontal sections (Pl. IV, fig. 31, *Ni.*) ; they do not lie in the fibres but belong to the syncytium through which the fibres pass.

Jourdan (35) gives a similar description of the elytra of Polynoe. He regards the fibres as secretion products of the epidermis, comparable with, but different from, the cuticle.* Darboux asserts that the fibres of the elytra are processes of epidermal cells, together with special sub-epidermal fibre-cells containing nuclei which, he asserts, have escaped Jourdan's notice. In *Aphrodite aculeata* the fibres clearly differ in character from the granular epidermal cells through which they can be readily traced to the cuticle.

Many of the Aphroditidae possess special sense organs on their elytra. In Polynoe they are somewhat similar to the papillae on the palps (Pl .III, fig. 26). Special sense organs are not present on the elytra of *Aphrodite aculeata*—an absence probably correlated with the enclosed conditions of these organs.

The glandular character of the epidermis of the dorsal fimbriated papillae has already been mentioned (Pl. III, figs. 18 and 19). Its elements are greatly elongated ; towards the basement membrane sub-epithelial cells and nerve fibres are abundant. The surface is devoid of sense organs or cuticular excrescences.

ANATOMY OF THE INTERNAL ORGANS.

In order to expose the integument of the dorsum it is necessary to cut through the felt and deflect the palps (Pl. I, fig. 1*a*). The worm may then be opened up by a median longitudinal incision in the dorsal body wall. The first puncture allows a quantity of fluid to escape. If the worms are sexually mature, masses of eggs or sperm will also ooze out.

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* Jourdan (35) gives the following quotation from Waldeyer (68) :—"Il faut encore faire ressortir, à propos des formations épitheliales, qu'elles sont capables de fournir une espèce de substance de soutien. Je ne considère comme telle les formations cuticulaires. Cette dernière expression ne doit pas etre prise dans un sens étroit comme une formation superficielle membraniforme. Je crois qu'entre les cellules épitheliales aussi il peut se former une excrétion durcissante, sous forme d'un réseau, excrétion qui functionne comme une charpente de soutien et qu'il faut placer à côté des formations cuticulaires des surfaces libres."

The coelom (Pl. IV, fig. 32) is a spacious cavity, divided into compartments by delicate fenestrated partitions termed septa, a definite segmental arrangement of the organs and muscles is noticeable between these septa.

The alimentary canal (Pl. IV, fig. 32.), with its paired diverticula (*Cae.*), occupies the greater part of the body cavity and obscures most of the other structures. The anterior part of the ventral nerve cord (*Nc.*) may be exposed by deflecting the shiny muscular pharynx (*Ph.*). A delicate colourless blood vessel (*Dv.*), giving off lateral branches, runs along the middle line immediately above the intestine. The nephridia are entirely hidden.

THE COELOM.

The body cavity of the Chaetopoda is a true coelom lined by peritoneum and typically divided by septa into a number of compartments corresponding to the external segmentation. In Aphrodite the septa are very delicate and are only readily visible towards the posterior end of the body (Pl. IV, fig. 32, *Sept.*). They consist of double folds of the coelomic epithelium, which also clothes the surfaces of all the organs in the body cavity. The alimentary canal is attached to the body wall dorsally and ventrally by median longitudinal mesenteries (Pl. V, fig. 38, *Mes.*), which thus divide the coelom into right and left compartments, but anteriorly both the septa and these mesenteries are so fenestrated that they become strands of tissue keeping the main blood vessels in position.

The peritoneum (Pl. IV, fig. 33*a*) is a thin transparent membrane formed of a single layer of cells, the walls of which are ill-defined. It is strengthened by a network of very fine straight fibres. At regular intervals it bears patches of ciliated cells (Pl. IV, fig. 33*b*) with definite walls. If a fragment of the tissue be examined in coelomic fluid, these patches are readily distinguishable by masses of corpuscles entangled between the bases of the cilia. The internal organs are bathed by a liquid, the coelomic or perivisceral fluid, which fills the body cavity. It is colourless and contains colourless amoeboid corpuscles. These amoebocytes or coelomic corpuscles (Pl. IV, fig. 34) are spherical or fringed with tiny pseudopodia. They are nucleated and contain pale yellowish globules and frequently also ingested solid bodies. When freshly examined the yellow globules exhibit Brownian movement.

The amoebocytes are derived from special groups of peritoneal cells which Cuénot (9) termed " lymph glands," and Darboux (15) named *amas lympathiques*. The innermost cells of the glands are regular and closely packed, whilst the edges of the peripheral cells are often seen projecting as tiny pseudopodia. These latter are freed into the coelom and become the amoebocytes. In Aphrodite the lymph glands are very numerous. They are developed both on the septa and on the sheaths of the blood-vessels. In addition to the amoebocytes, the coelomic fluid contains small, colourless discoidal bodies.

The function of the coelomic fluid has been compared to that of the lymph of vertebrates. It subserves three purposes. The leucocytes or coelomic corpuscles ingest solid waste products and they are then passed to the exterior by way of the nephridial tubes. The other two more important activities are connected with respiration and nutrition. Constant waving of the peritoneal cilia and rhythmical respiratory movements of the body, together with all locomotory activities, combine to keep the coelomic fluid in continual motion and thus ensure the distribution of nutritive products and oxygen to all parts of the body. The occurrence and relative value of these factors vary in different Annulates. For example, in forms such as Arenicola, undulatory movement of the whole body is the chief agent in keeping up the perivisceral circulation, as here the peritoneum is devoid of cilia. In creeping forms such as the Hermioninae, undulatory movements are almost entirely confined to the dorsal surface in connection with which the elytra are developed.

The coelomic fluid also ensures turgidity of the body. This is important in the protrusion of the pharynx, movements of the feet, etc.

In addition to the perivisceral circulation, many Chaetopoda possess a closed system of canals forming the vascular system and containing a fluid whose red colour is due to the presence of haemoglobin. Huxley (31) termed this fluid " respiratory blood," an opinion of its function which is supported by Beddard (5) and others. In *Aphrodite aculeata* the blood system is very delicate and its fluid is colourless. Haemoglobin does, however, occur. The red colour of the nervous system has already been noted (see page 6). Lankester (41) has proved it to be due to the presence of haemoglobin. It is noteworthy that the pigment is confined to this situation.

BLOOD SYSTEM.

Though the arrangement of the blood system of the Aphroditidae conforms to the general plan characteristic of Polychaets, the colourless condition of the fluid, combined with the great fragility of the walls of the vessels themselves, led many of the early investigators to deny the existence of a circulatory system in the elytra-bearing worms.

The course of the vessels is difficult to follow unless injected specimens are employed. Large specimens are required and considerable numbers and, as there is no reason to doubt the excellent work and description of Selenka (57), the following account has been based on his researches.

Most of the principal vessels can be followed in maturing females when the walls of the blood-vessels are thickened by masses of developing sex cells (Pl. VII, figs. 57 and 59).

The two largest and most readily distinguishable vessels lie in the axial plane and extend from the anterior to the posterior end of the animal. One lies above the alimentary canal and is termed the dorsal vessel (Pl. IV, fig. 32, *Dv.*), and the other, the ventral vessel, is situated beneath it. Anteriorly and posteriorly the two vessels bifurcate and their branches fuse to form ring-like vessels encircling, respectively, the buccal mass and the anus, and giving off branches to the surrounding structures.

The blood flows forwards in the dorsal vessel, but special pumping organs such as are found in connection with this vessel in many Polychaets are entirely absent.

The lateral branches of the dorsal and ventral vessels are segmentally arranged. From the dorsal vessel the blood is distributed to all parts of the body. It is then collected and conveyed to the ventral vessel in which it flows backwards. Eventually, after circulating in the respiratory anal rosette, it again reaches the dorsal vessel. This vessel, where it overlies the pharynx, is free and unbranched. But posterior to the oesophagus it is attached to the alimentary canal by a median longitudinal plexus (Pl. V, fig. 38), which gives off numerous ring-like vessels encircling the intestine and passing into the ventral vessel. This intestinal plexus of annular vessels is the chief connection between the dorsal and ventral vessels.

Lateral Vessels.

In each segment posterior to the pharynx a group of vessels arises from the dorsal vessel and passes upwards in the mesentery of the alimentary canal (Pl. V, fig. 38, *Dp.*). Immediately beneath the dorsal longitudinal muscles these vessels form a plexus from which branches pass outwards to the body wall, the caeca, the nephridia and the muscles. Repeated branching of the vessels leads to the formation of capillary nets which surround the organs. These capillary networks are developed round the caeca, the nephridia and the notopodial and neuropodial muscles. The main vessel supplying the nephridium is expanded into a little pear-shaped sac lying against the wall of this organ (*Ht.*). Selenka termed these structures " hearts." The lateral groups of vessels of the two sides of the body are connected by a ventral plexus (*Vp.*), which lies just above the ventral longitudinal muscles.

Blood is returned from the organs to the ventral vessel by many branches which join up and run in the intersegmental septa. They are termed lateral plexi (Pl. V, fig. 38, *Lp.*). The lateral plexi are very well developed in the posterior region of the body where the septa are intact. Anteriorly the septa are represented by strands of peritoneum running between the necks of the caeca.

The " Hearts."

These swellings in connection with the nephridial vessels are readily distinguishable as little oval sacs with indented walls. They lie in contact with the nephridia where these organs curve round the neuropodial setal muscles. They are distinctly white in contrast to the yellow colour of the nephridial tube (Pl. VIII, fig. 65, *Ht.*). I find that the structure of their walls (Pl. IV, fig. 37) resembles that of the ventricle and " heart body " of Arenicola, described by Ashworth (3). The cavity is lined by a delicate endothelium (*e.*) and is surrounded by a muscle layer of circular fibres (*Mc.*). Folding of the wall greatly reduces the lumen. The muscle coat is clothed by coelomic epithelium (*P.*), the cells of which are large, vacuolated and granular. They fill in the spaces between the folds.

The heart body of the Polychaets in connection with the dorsal vessel was first discovered by Claparede, in 1873. It has since been found to be a characteristic Polychaet organ and numerous theories have been advanced to explain its function. Cuénot (9) believed that it was a lymphatic organ destined to manufacture haematids for the blood stream. He therefore termed it the " cardiac gland." Their function in Aphrodite is unknown. Their structure does resemble that of the heart bodies of Arenicola. But in Aphrodite their intimate relations with the nephridia are peculiar. Possibly they form certain constituents of the blood, although coloured haematids are absent.

The functions of the blood are very much reduced in Aphrodite. It is largely the coelomic fluid which subserves respiration and nutrition. In this connection it is interesting to note that Selenka, in injecting the blood system, found it impossible to trace the smaller capillaries either into the integument or into the walls of the intestine. His injection masses always ceased abruptly before they reached these surfaces. The author has failed to find any traces of vessels in sections of these structures.

RESPIRATION.

In the Annelids the exchange of gases takes place over the whole surface of the integument. Bounhoil (7) confines the term true gills or " branchiae " to structures which carry out more than 75 per cent. of the whole respiratory activity of the individual. According to this view the number of Polychaets which possess branchiae is comparatively small. The definition makes a line of demarcation between these forms and the large assemblage of worms which exhibit modifications such as integumentary folds and papillae, destined to increase the respiratory area, but in which respiration is not more active than over the general body surface. The so-called branchiae of Cirratulus belong to this group.

When the blood is red the colouration is due to the presence of haemoglobin.

Some Polychaets are well supplied with respiratory pigment. *Leprea* (*Terebella*) *lapidaria*, for example, has coloured corpuscles both in the blood and in the coelomic fluid. Others, for example the Glyceridae, are devoid of a vascular system. Both respiration and nutrition are entirely carried out by the coloured coelomic fluid, which is kept in continuous circulation by definite ciliated tracts of an otherwise non-ciliated peritoneum.

The Aphroditidae and the Syllidae represent an intermediate condition. They possess a vascular system, but the blood is colourless and probably plays little if any part in respiration. The coelomic fluid, which is also colourless, serves both for respiratory and nutritive purposes.

In the elytra-bearing worms the integument is more or less specially differentiated on the dorsal and ventral surfaces. In the Hermioninae the ventral body wall is thickened as an adaptation to the creeping mode of progression and its respiratory activity is reduced, so that the function is carried out by the thin dorsal body wall. The surface area of the dorsum is considerably increased by the projecting dorsal tubercle and elytrophores. It is protected by an armour of plates, the elytra, which are firmly fixed and more or less closely applied to the surface.

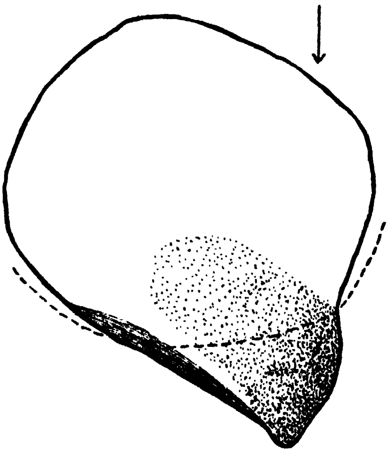
These elytra exhibit a rhythmical movement which ensures the continual change of the surrounding water. A comparison of these movements in Aphrodite and Hermione is interesting. In the latter genus there is no dorsal felt, so that the movements of the elytra can be readily examined. Also, Hermione is much more easily kept in aquaria.

In Hermione the tips of the last pair of elytra meet in the middle line and project beyond the anus, to form a little spout-like pouch (Pl. IV, fig. 36, *Eb*[1].). If a living specimen be watched a rhythmical opening and closing of this orifice is readily distinguishable; it is brought about by the lateral movement of the last pair of elytra. Closer examination of the dorsum reveals an undulatory movement which commences at the anterior end and increases in intensity as it passes posteriorly. It culminates in the opening of the orifice and the forcible ejection of a jet of water. Almost at once the aperture is closed and the rhythm recommences.

It is practically impossible, except at the posterior end, to detect any individual movement of the elytra separate from an elevation and depression in which the whole dorsum appears to take part. The undulation is most intense in the sagittal plane. The opening and closing of the posterior aperture is very regular. In specimens examined for several hours the ejection of water occurred every three or four seconds.

Similar respiratory movements take place in Aphrodite, but the action is subject to long periods of suspension. The length of time most constantly observed to elapse between successive ejections varied between 30 and 50 seconds. It is, however, probable that these periods, observed in aquarium specimens, bear little relation to the actual-time values under natural conditions. Aphrodite is not a shore form and it rarely lives in confinement for more than five or six days.

The ejection apparatus of Hermione is formed by a special modification of the last pair of elytra. The total number of segments in this genus is 32 or 33. The fourteenth pair of elytra are borne on segment XXVII and the fifteenth and last pair are attached to segment XXX, so that posterior to this there are only three segments. The last pair of elytrophores are considerably enlarged; and the elytra and their areas of attachment are elongated in an antero-posterior direction; also, the elytra project beyond the end of the body and where they meet in the sagittal plane they form the little pouch already noticed. The projecting portions of each of the pouch-forming elytra (Text-fig. 5) are brown in colour and considerably thickened; also, the fan-wise group of spines (Pl. IV, fig. 36, *S.*) are absent from the last elytrous segment.

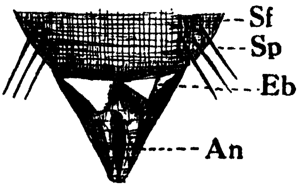


TEXT-FIG. 5.

Quite a different arrangement occurs in Aphrodite. In this form the nine to twelve segments posterior to the last pair of elytra are very small (Pl. I, fig. 1*b*) and they form a distinctly pointed tip, which is supplied with a sensory fringe formed by the elongated notopodial cirri of the parapodia. This highly sensitive terminal region is very mobile and it is usually held in an upturned position (Pl. IV, fig. 35). It forms the mechanism which controls the ejection of water from beneath the elytra.

The felt, by reason of its lateral origin, is open at the anterior and posterior extremities and also between the segments. It is considerably thickened near the posterior end. The anus and the edges of the last pair of elytra can extend beyond the felt; the elytra are elongated posteriorly but they are otherwise unmodified.

When the upturned anal extremity expands, it tends to assume a horizontal position (Text-fig. 6) and its tip, projecting beyond the edge of the felt, is depressed from beneath the elytra; and thus an opening—the ejection aperture—is formed. The aperture is closed by an elevation and contraction of the terminal segments in such a way that the tip is drawn up beneath the elytra and against the edge of the felt.



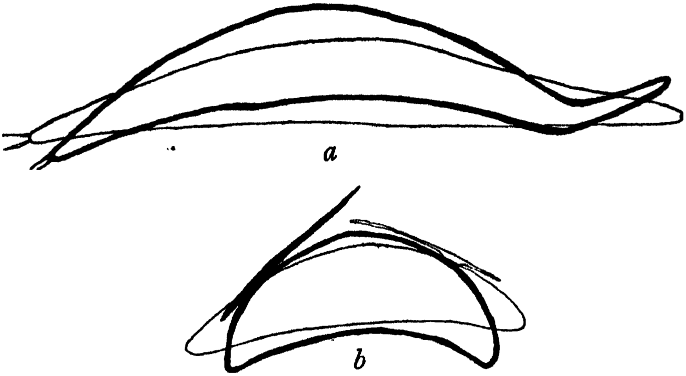
TEXT-FIG. 6.

The connection of the periodic ejection of water with movements of the elytra can often be detected through the felt. A regular elevation and depression of the dorsum alternates with the contraction and expansion of the anal extremity. When the felt is raised the posterior aperture is closed (Pl. IV, fig. 35); when it is depressed the sensory tip expands and a jet of water is forced out through the orifice. But if the felt be slit along the middle line the part played by the elytra in this circulation of the water can be more closely followed. After cutting through the felt it is necessary to allow the animal to rest, but in a well-aerated tank the movements of the elytra soon assume a marked regularity.

The elytra are held in an elevated position whilst the posterior aperture is closed. Often no movement takes place for a considerable time. The first indication of activity is given by a slight depression of the anal extremity, almost at once rapid movements elevate the elytra to their maximum extent and open the ejection aperture. Depression of the scales follows immediately; it begins with the anterior pair and passes backwards in such rapid succession that the right and left series of elytra appear to close down on to the dorsum like the two halves of a casement window. The flattening of the elytra on to the dorsum forces a considerable jet of water out from the ejection apparatus, after which it immediately closes and the elytra are again elevated. Whilst the water beneath the felt is being rhythmically pumped out by way of the ejection apparatus, a fresh supply is continually percolating in through the felt. The respiratory movement is not entirely confined to the elytra themselves. Two flexures of the body play an important part in elevating the scales. One is an antero-posterior flexure of the trunk (with the exception of the posterior extremity) with its concavity ventralwards (*a*). The other flexure is at right angles to this; its concavity is also ventralward, by it the right and left margins of the body are drawn slightly together below (*b*) (Text-fig. 7).

All these movements which are ensuring change of the external medium also help to keep the coelomic fluid in circulation and thus bring about the distribution of oxygen to all the organs in the coelom.

Darboux (15, p. 162) states that the amount of movement of the elytra is small but definite. He says that " Il est facile, sur un Aphroditien en repos, de constater que chaque élytre s'élève et s'abaisse alternativement et que le mouvement se produit successivement sur les paires successives, de la première à la dernière ; le résultat est facile à prévoir : il se produit sur la face dorsale un courant d'eau continu, assez vif, et c'est par suite dans un milieu extern sans cesse renouvelé que se trouvent placées les branchies lympathiques sur la face dorsale."



TEXT-FIG. 7.

This statement is quoted by Bohn (6) and from it he developed the theory already quoted (see p. 18). We think that this statement is much too general. In *Lepidonotus clava* (Montague), for example, we have been unable to detect this separate movement of the elytra. Haswell also states that *Polynoe argus* from Port Jackson habitually rests with its elytra in an elevated position. He denies that there is any movement in some of the species of Polynoe when at rest—and states that in general the movement of the elytra is in abeyance in non-felted forms.

THE DIGESTIVE SYSTEM.

A. GENERAL FORM.

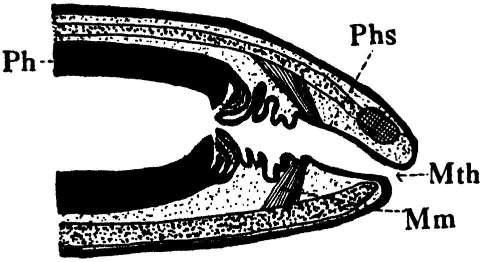
The remarkable shape of the alimentary canal (Pl. IV, fig. 32) has been described by many workers. Its most striking features are a large rigid and shiny muscular pharynx (*Ph.*), and the numerous paired diverticula (*Cae.*)

of a peculiar and characteristic shape which are given off from the intestine (*Int.*).

The canal may be divided into three regions. The most anterior division, termed the Pharyngeal Region, stretches from the mouth to the origin of the first pair of diverticula (Pl. IV, fig. 32, *Cae.* 1). This is followed by the Intestinal Region which extends to the base of the last pair of diverticula. The posterior region, the Rectum, comprises the short unbranched extremity of the canal and terminates at the anus (*An.*). The anterior and posterior regions are of ectodermal origin, whilst the intervening intestinal division is derived from the endodermis.

I. The Pharyngeal Region is chiefly concerned with the reception of food, to which function its structure is intimately related. It consists of three sections, each of which plays a special part in the eversion of the pharynx.

The mouth (Text-fig. 8, *Mth.*) leads into a chamber termed the Buccal Cavity, the walls of which are soft and much folded, and form a structure which is present in most Polychaets and is generally termed the Buccal Mass (*Phs.*). The second division consists of the cylindrical Pharynx (Pl. IV, fig. 32, *Ph.*) ; its walls are rigid and very thick. When viewed from above the greater part of the buccal mass is hidden by the pharynx, but its posterior limit is



TEXT-FIG. 8. Diagrammatic longitudinal section through anterior region of body to left side of median line—illustrating motor muscles of pharynx.

marked by a narrow band (incomplete laterally) of iridescent muscles (Pl. IV, fig. 32 *Sb.*). In fresh specimens the distinct red colouration of this region is due to the stomato-gastric nerves (see p. 74) The wall of the pharynx is marked by circular bands which become less definite posteriorly until, where the tube narrows, they are replaced by longitudinal striations. This narrowed region is bent into the form of an S and is termed the Oesophagus (*Oes.*). The Oesophagus is co-extensive with a number of band-like muscles which stretch from the posterior end of the pharynx to the junction of the oesophagus with the intestine. These muscles (Pl. VI, figs. 48 and 50, *Ms.*) were termed *Muscles amortisseurs* by Darboux, in allusion to their function. The protrusion of the rigid pharynx through the mouth draws the flexible buccal mass forwards and causes it to turn inside out so that it forms a sheath covering the projecting end of the "proboscis" (Pl. I, fig. 2, *Phs.*). On this account Darboux designated the buccal mass by the appropriate term "pharyngeal sheath." The forward movement of the pharyngeal region straightens out the oesophageal bend and brings into play the *muscles amortisseurs* which, acting as shock absorbers, draw the intestine forwards also, and prevent it from tearing away from the oesophagus. In Polychaets which totally protrude the "proboscis" there is a much greater development of "shock absorbing" muscles.

Mechanism of Eversion of the Pharynx.

The pharyngeal sheath is connected to the body wall by two pairs of muscles termed the dorsal and ventral motor muscles (Text-fig. 8, *Mm.*). They are inserted into the body wall in the intervals between the two rami by which each of the dorsal and ventral longitudinal muscles arises. Except for these muscles the pharyngeal region is quite free in the coelom, whereas the intestine is connected to the body wall by a pair of mesenteries which lie in the axial plane (Pl. V, fig. 38, *Mes.*).

The eversion of the pharynx is chiefly dependent on the pressure of the coelomic fluid, due in part to the muscular contraction of the body wall. The motor muscles (Text-fig. 8, *Mm.*) contract and thus tend to draw the middle and posterior regions of the pharyngeal sheath towards the mouth. Contraction of the body of the worm causes the coelomic fluid to flow towards the anterior end, and an increase in pressure results. This increase in pressure, quite apart from the direct action of motor muscles, simultaneously causes the expansion of the inferior lip (Pl. I, fig. 2, *Li.*) and the expulsion of the pharynx through the mouth. As the largest part of the pharynx passes out the pressure of fluid in the coelom is reduced, the tissues of the inferior lip relax and thus, as it were, clamp the pharynx in its extruded position. The motor muscles, after their primary contraction, may be regarded as being passively extended to their maximum when eversion is complete.

Retraction of the organ is initiated by a contraction of the motor muscles which disturbs the condition of equilibrium arrived at between the pressure of the coelomic fluid and the elasticity of the muscles involved.

II. The Intestinal Region (Pl. IV, fig. 32, *Int.*) is concerned with digestion. It is thin-walled and yellow in colour. After a short course of about one-and-a-half inches it expands abruptly and attains its greatest diameter about the middle of its length, then it gradually narrows towards the anus. In each segment it gives rise to a pair of pouches. Typically there are 18 to 20 pairs of these diverticula, termed intestinal caeca (*Cae.*), arising from the dorso-lateral walls of the intestine. The anterior pair belong to segment VIII and the last two or three pairs lie in segments XXVI to XXVIII.

The first eight pairs of caeca are given off at very close intervals, they are directed anteriorly to their respective segments. The others are more evenly spaced and pass out at right-angles to the intestine.

Each caecum (Pl. V, fig. 39) may be divided into four regions. At the base there is a little pyramidal sac which, on account of its function (see p. 51) may be termed the sieve (*Sa.*). A narrow tube, termed the neck (*Nk.*) connects the sieve with a large expansion, the dorsal sac (*Ds.*). The dorsal region of the sac gives off a number of blind diverticula which are closely apposed to the walls of the dorsal tubercle (or elytrophore) in which this region of the caecum is situated (Pl. V, fig. 38, *Cae.*). The distal end of the dorsal sac is narrowed as it turns towards the ventral body wall, against which it expands, to form the unbranched ventral sac (Pl. V, fig. 39, *Vs.*). These terminal portions of the caeca can be clearly seen by pushing the intestine over to one side (Pl. IV, fig. 32, *Vs.*).

Owing to the extreme thinness of the walls of the caeca the dark brown colour of their contents is clearly visible. The shape of the caeca varies slightly in different regions of the trunk. In the anterior regions the necks are greatly elongated. The dorsal sacs of the posterior pairs bear very few diverticula. In individuals possessing twenty pairs of caeca the two most posterior pairs are usually simple unbranched pouches.

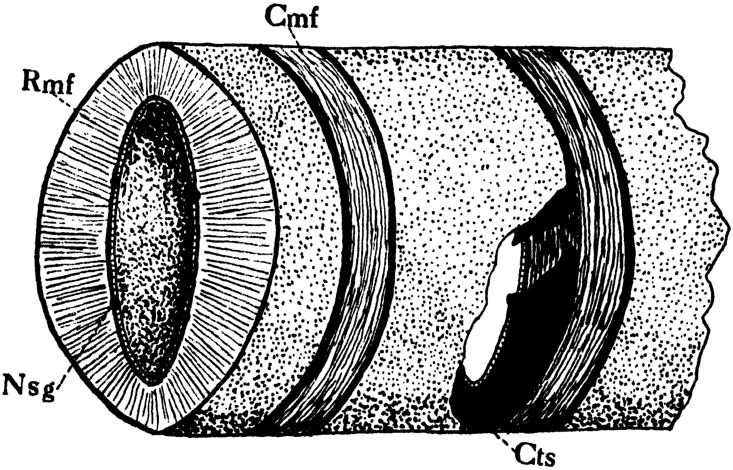
B. HISTOLOGY.

I. *Pharyngeal Regions.*

The Buccal Mass. The buccal cavity is lined by a very thick cuticle (Pl. V, fig. 40, *C.*), which is responsible for the marked iridescence of this region. Underlying the cuticle is a layer of columnar epithelium (*Ce.*) interspersed with gland cells (*Gc.*) provided with little ducts which pass through the cuticle.

The epithelium rests on a well-defined basement membrane (*Bm.*) formed by a dense network of fine interlacing fibres (see p. 22). The basement membrane is surrounded by a muscle coat which chiefly consists of circular fibres (*Mc.*) external to which is an incomplete layer of longitudinal muscles. The whole structure is enclosed by the peritoneal sheath (*P.*).

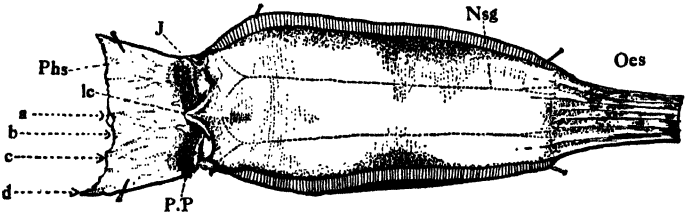
The cavity of the Pharynx (Pl. V, fig. 41), like that of the buccal mass, is lined by cuticle which, however, is comparatively thin. Below the cuticle lies an epithelium of elongated columnar cells (*So.*) richly interspersed with masses of gland cells (*Gc.*). Branches of the stomatogastric nervous system (see p. 74) run through the epidermis, they are seen in the positions marked in Text-figs. 9 and 10 (*Nsg.*). The basement membrane (Pl. VI, fig. 47, *Bm.*) gives off projecting tags (*TBm.*) which lie between the bases of the epithelial cells and between the elements of the muscle coat surrounding it. The structure of the thick muscle coat of the pharynx is best described by reference to Text-fig. 9. It is made up of a series of



TEXT-FIG. 9. (The outer connective tissue sheath has been removed.)

segments composed of radial muscle fibres (*Rmf.*) alternating with thin discs of circular muscles (*Cmf.*). The muscle segments are separated from one another by thin connective tissue septa (*Cts.*) which are joined both to the basement membrane and to a thick outer sheath (Pl. V, fig. 41, *Ots.*) of connective tissue which encloses the muscle coat. The coelomic surface is clothed by the peritoneum (*P.*).

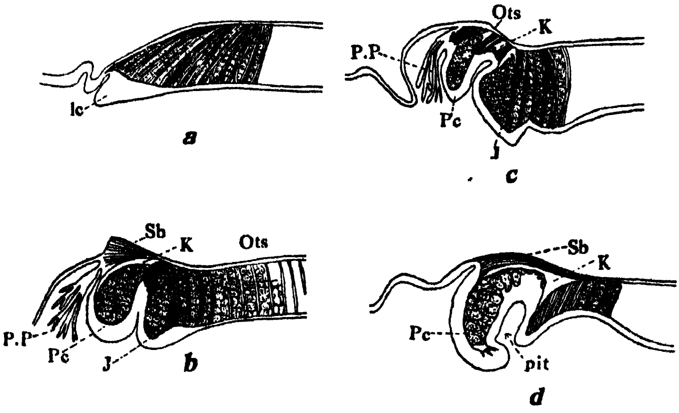
In the anterior region of the pharynx this regular alternation of circular and radial muscles is interrupted by the presence of jaws and papillae, which, in a state of retraction, lie within its lumen. These structures are best seen by removing the whole of the pharyngeal region from the body cavity and slitting it up along the mid-dorsal line. Text-fig. 10 represents the right half of this region looking into the lumen. The papillae (*P.P.*) are pale yellow in colour and they form a conspicuous fluffy band lying at the anterior limit of the pharynx. They arise from a muscular ridge (termed for convenience in description the papilla cushion (*Pc.*)) which lies just within the shiny band of muscles already seen from the external surface (Pl. IV, fig. 32, *Sb.*). The circle of papillae is divided into four segments each containing from 14 to 20 tufts or groups (Pl. V, fig. 42). Each tuft has a muscular stem which gives rise to a number of finger-like processes exhibiting a roughly dichotomous branching.



TEXT-FIG. 10. × $\frac{4}{3}$.

The jaws (Text-fig. 10, *J.*) are four in number ; each one is essentially a pyramidal muscular hump and thus is quite unlike the brown chitinous teeth of Nereis. Along the mid-dorsal and mid-ventral line the wall of the pharynx is comparatively thin, but laterally, between the jaws, it is greatly thickened to form pads which may be termed the lateral cushions (*lc.*). This arrangement permits the pharynx to be flattened from side to side. The lumen is thus reduced to a mere slit and great pressure may be exerted on its contents. Owing to the presence of the jaws and the papilla cushion, the epithelium and associated layers are thrown into two folds separated by a ring-like depression. This folding does not affect the outer sheath, which is here strengthened by muscles (Pl. IV, fig. 32, *Sb.*). The arrangement is interesting as it demonstrates the action of the papillae and jaws during the eversion of the pharynx.

This is readily explained by reference to Text-fig. 11 (*a, b, c, d*) which is a diagrammatic representation of four radial longitudinal sections in the positions indicated by the dotted lines *a, b, c* and *d,* in Text-fig. 10.



TEXT-FIG. 11. Four radial longitudinal sections through wall of pharynx—anterior end.

In Text-fig. 11, section *a* passes through the centre of the lateral cushion (Text-fig. 10, *a*). The thickness of the wall is made up of circular and radial muscle discs which pass obliquely backwards from the basement membrane to the outer sheath. The projecting tip of the lateral cushion (*lc.*) is composed of elongated epithelial cells.

Section *b* cuts the end of one of the four segments of the ring of papillae (Text-fig. 10, *b*). Bundles of circular muscle fibres form the mass of the papilla cushion (Pl. V, fig. 43, *Pc.*) and of the jaws (Pl. V, fig. 45, *J.*).

Section *c* passes through the tip of the jaw (Text-fig. 10, *c*).

Section *d* is mid-ventral and passes through the median projection of the papilla cushion (Text-fig. 10, *d*), where the papillae are absent. It illustrates the thinness of the wall of the pharynx in the axial plane.

By a comparison of the diagrams *a, b, c* and *d*, it is apparent that the circular muscles of the papilla cushion are most strongly developed in the mid-dorsal and mid-ventral lines (*d*) where the jaw muscles are practically absent. These two groups of muscles are separated by a space from the connective tissue sheath (*Ots.*). This space (*K.*) is traversed by a number of strands of muscles (*M.*) which connect the lining epithelium to the outer sheath (*Ots.*). When the " proboscis " is protruded the papilla cushion and the jaws are caused to lie in the same vertical plane and the pit (*pit.*) which separates them in the retracted state is obliterated. This causes the papillae to project forwards as a fringe surrounding the " mouth " of the " proboscis " (Pl. I, fig. 2, *P.P.*).

The papillae are essentially folds, involving the whole thickness of the wall at the junction of the buccal mass and the pharynx. Each bunch of papillae has a core of muscle fibres which extends almost to the tips of its branches (Pl. V, fig. 44, *M.*). Sections (Pl. V, fig. 43, *Pb.*) through the pharynx at the bases of the papillae clearly illustrate this structure. The cuticle covering the papillae is very thin. The epithelium (Pl. VI. fig. 46) resembles that of the buccal mass and consists of columnar cells (*Ce.*) with large nuclei interspersed with numerous gland cells (*Gc.*), with ducts (*Gd.*) passing through the cuticle. The fibre-like basement membrane lies between the bases of the epithelial elements and occupies the cores of the papillae and surrounds the muscles (*M.*). The papillae have no central cavity. In this character they differ markedly from the figures of the papillae of *Lagisca rarispina* given by Darboux. This worker describes a series of cavities in the papillae which fuse to form canals opening at the tips of the jaws. He suggests that a similar condition may be present in *Aphrodite aculeata*, but this is not so. All the glandular elements of the papillae discharge their secretion directly by ducts passing through the cuticle (Pl. VI, fig. 46, *Gd.*).

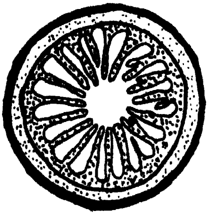
The epithelium and associated layers which line the pharynx anteriorly are of considerable thickness (Pl. VI, fig. 47). The depth of the cuticle varies greatly but is, everywhere, inconsiderable when compared with that of the epithelial elements themselves. The supporting cells of the epithelium (*So.*) are almost fibre-like. Their nuclei lie close to the cuticular border. Gland cells are numerous. They are club-shaped with elongated necks passing through the cuticle. They are very closely packed on the papilla cushion (Pl. V, fig. 43, *Gc.*), but certain other areas of the epithelium consist only of supporting cells—as, for example, the tips of the jaws. The gland cells are generally filled with mucus, empty cells are rare. The basement membrane is characterised by projecting tags which lie between the bases of the epithelial cells (Pl. VI, fig. 47, *TBm.*) and between the muscle fibres.

The epithelium lining the oesophagus is thrown into longitudinal ridges which develop gradually from before, backwards. These folds, together with the narrowing of the tube, greatly reduce its lumen posteriorly (Pl. VI, fig. 48). The cells of the epithelium (Pl. VI, fig. 49) consist of supporting cells (*So.*) and gland cells (*Gc.*), both of which are elongated in the region of the folds. In sections, numerous pale patches at the base of the epithelium (Pl. VI, fig. 48, *Nsg.*) are noticeable—these are the cut ends of stomato-gastric nerves.

The oesophagus differs from the pharynx chiefly in its musculature which consists almost entirely of segments of circular muscles (Pl. VI, figs. 48 and 50, *Mc.*) separated from one another by connective tissue septa. A few of these septa appear to be double and to enclose radial muscle fibres, thus recalling the arrangement of the muscles of the pharynx. The thickness of the muscle coat decreases considerably towards the posterior end of the oesophagus (Pl. VI, fig. 50, *Cn.*). The outer connective tissue sheath (*Ots.*) is continuous with that of the pharynx.

II. *The Intestinal Region.*

In fresh specimens the epithelium of the intestine is bright yellow in colour. In the short, narrow anterior region it is much folded and forms a fine filtering apparatus (Text-fig. 12) immediately behind the ends of the folds of



TEXT-FIG. 12.

the oesophagus (Pl. VI, fig. 50). The lining of the rest of the intestine forms folds or papillae which are very irregularly distributed. The epithelial cells are all of one kind. Each is an elongated cylinder, slightly expanded at its free margin ; the oval nucleus lies near the base. In fresh preparations the cells are packed with small oily yellow globules, in sections (Pl. VI, fig. 51, *Ie.*) they are evenly granular. Scattered round gland cells occur between the bases of the granular elements (*Gc.*). The basement membrane (*Bm.*) is well defined, it is surrounded by two muscle coats, the inner one consisting of discs of circular muscles (Pl. VI, figs. 50 and 51, *Mc.*) separated by thin plates of connective tissue. This layer is enclosed by a coat of longitudinal muscle fibres (*Lm.*) to which the *muscles amortisseurs* already described (Pl. VI, figs. 48 and 50, *Ms.*) are attached. The outer sheath (*Ots.*) of the pharyngeal region ceases at the commencement of the intestine, so that here the peritoneum surrounds the longitudinal muscles.

Each caecum commences with a small chamber (Pl. V, fig. 39, *Sa.*), the sieve. Within it the epithelial cells are modified in a remarkable manner. They are elongated in such a way as to form two plates (Pl. VI, fig. 52) which project into the lumen from opposite walls. This reduction of the internal cavity forms an effective filtering apparatus which prevents any but the finest particles from entering the caecum. The bases of the caeca are surrounded by sphincters formed by the circular muscles of the intestine.

The cells of the caecal epithelium are clothed with short dense cilia (Pl. VI, fig. 53). In fresh preparations these cells are packed with small yellow globules like those of the intestinal epithelium, but beyond the sieve the character of the epithelium is markedly different from that of the intestine.

A portion of the caecal epithelium is illustrated in figure 54 (Pl. VI). The cells are elongate, with narrow bases and expanded free surfaces. On a general examination of either fresh preparations or sections, two chief types of cells are readily recognised.

I. Cells (Pl. VI, fig. 54, *I.*) with regularly vacuolated protoplasm, many of which contain irregular masses of brownish granules in their expanded ends. In sections these cells are pale in colour; fresh cells are filled with pale yellow oily globules.

II. Cells containing a variable number (5 to 20) of large spherules which stain strongly with eosin (Pl. VI, fig. 54, *II.*). The cytoplasm is non-vacuolated and densely granular, especially towards the bases.

The distribution of these two types of cells is quite irregular; the epithelium forms papillae some of which consist almost exclusively of one or other of these types, whilst others contain both kinds of cells in approximately equal numbers. In the epithelium of the ventral sac cells of the first type often predominate over those of the second. In general the cells lining the necks of the caeca are more cubical (Pl. VI, fig. 52, *Nk.*).

Because of extremely conflicting opinions regarding function, it is important to note the details of the different types of cells forming the caecal epithelium.

The following description refers to cells illustrated in figure 55 (Pl. VII). These are all representative examples of cell types present in great numbers. They are demonstrable in preparations fixed and stained by a variety of methods.

Figure 55. Types I to XI.

Type I. These are club-shaped cells with regular outlines. They never attain the maximum height of the papilla. The cytoplasm is dense, finely granular and non-vacuolated; it stains deeply. The nuclei have well-defined nucleoli and lie towards the bases of the cells.

Type II resemble type I in the characters of the cytoplasm, but they are larger and more expanded. The distal (or free) end of the cell bears numerous large vacuoles, each of which is occupied by a shiny spherical globule (*eg.*). These globules stain strongly with eosin or Mallory's connective tissue stain and their bright red colour forms a striking feature of the epithelium. In preparations treated by the latter method, the cytoplasm immediately surrounding the globules exhibits a distinctly blue tint, in contrast to its typical pink colour elsewhere. In examining the globules in detail it is possible to trace a complete series of colour changes from red to blue. Some of the red globules exhibit a peripheral blue ring which becomes successively thicker till the red coloured area is reduced to a tiny central spot and eventually disappears. The surfaces of the blue globules are distinctly less smooth than those of the red ones. Examples of further changes are very rare but it is, however, possible to find cells in which the blue globules appear to be breaking down to form a blue-grey granular mass lying in a large distal space formed by the fusion of originally separate vacuoles.

Illustrations III, IV and V are various forms of type II. They all have regular cell walls and differ only in the arrangement of the globules.

Type VI is drawn from a single example. The cytoplasm is finely granular and vacuolated. Some of the vacuoles contain small blue-grey globules, but the majority are colourless. Although the above described changes are most readily distinguishable in preparations treated with Mallory's connective tissue stain, they can also be made out in sections stained with haematoxylin-eosin. Types VII to X are characterised by marked vacuolation of the protoplasm. Type VII occurs in great numbers, especially in the dorsal sac and its diverticula. Type VIII differs from it only in shape. It is characteristic of the cubical cells of the necks of the caeca. The cytoplasm is finely and evenly granular ; it contains numerous larger and more deeply staining granules (*bg.*) of somewhat irregular outline.

In Type IX these granules are much more numerous. Distally they form a dense mass, through which the borders of the vacuoles are scarcely distinguishable.

In Type X the granular mass is absent—only those granules remain which are attached to the periphery of the vacuole. In areas where these cells are abundant masses of granules lie in the lumen of the caecum. Similar granules are not present in globule-bearing cells (II to V).

In fresh preparations globule-bearing or eosinophilous cells (II, etc.) are readily distinguishable from vacuolated cells (VII, etc.). These latter (type XI) have a characteristic structure. The cytoplasm is packed with regular yellow spherules and the spaces between them are filled with smaller, more deeply coloured globules, like those which form the intestinal epithelial cells. Many of the larger spherules contain a small central crystal-like body. The contents of the caeca contain many free spherical bodies exhibiting this characteristic structure (XII). Darboux termed them " *ballots d'excretion.*"

Darboux (15) describes and figures three kinds of cells in the caecal epithelium.

I. *Secretory cells*—those which contain eosinophilous globules (fig. 55, II-V).

II. *Excretory cells*—with vacuolated protoplasm and bearing yellow-brown granules (fig. 55, VII-X).

III. *Undifferentiated cells* (fig. 55, *I.*) which do not contain granules or globules. Darboux regards these cells as young elements which give rise to both the above-mentioned groups I and II. He compared the function of the caeca with that of the digestive gland of some Molluscs in which similar cell types are recognisable.

Darboux based his opinion of the excretory rôle of the vacuolated cells on results obtained by injecting coloured fluids into the coelom of *A. aculeata.* Various injection fluids, such as indigo carmine and methyl green, were employed. After a considerable time the animals were opened and it was found that the caeca were distinctly coloured. Examination of the cells showed that the coloured matter was present only in the vacuolated cells. Darboux also found that certain other coloured liquids, such as ammoniacal carmine, were not absorbed by the caecal epithelium, but were taken up by the cells of the nephridia. Uric acid and its derivatives were found to be absorbed by the caeca and nitrogenous substances were excreted by the segmental organs. Darboux regarded the " ballots d'excretion " as the cut-off ends of excretory cells by which waste products were passed to the exterior. The secretory function of the eosinophilous cells was also based on experimental evidence.

Sellier (59), working also on this polychaet, demonstrated that protein digestion is carried out by the secretion of the caeca. This evidence supports that of Darboux and Krukenberg.

In a later paper, Jordan (33) believed that it was possible to find a complete series of cells linking up the secretory and excretory elements described by Darboux. He considers that absorption and secretion are the chief functions of the caeca and that excretion is purely incidental and not a separate function of a special cell type.

Jordan figures cells similar to those illustrated in figure 55, I, II, III, VII, as a series of stages in the development of "*fermenzellen*" or secretory cells (marked respectively S_1, S_2, S_4, S_6, in his figure).

The transitional stage (Jordan, S_5) between Darboux's secretory and excretory elements is a cell which contains eosinophilous globules towards the base and colourless vacuoles in the expanded distal end. Finally (Jordan, S_8), the distal ends of the cells are constricted off to form spheres filled with ferment which is thus conveyed to the lumen. The undifferentiated cells of Darboux (fig. 55, *I.*) are regarded by Jordan as cells responsible for absorption. The recognition of their absorptive function is based chiefly on experimental evidence since, histologically, they differ very little, except in size, from the later stages (Jordan, S_6) in the development of secretion cells.

Jordan fed Aphrodite with compounds containing iron and found that iron vacuoles were present in the absorption cells of the caeca, and nowhere else. He concluded, therefore, that these cells alone absorbed the nutrient products of digestion, but he was unable to state whether they were continuously individual throughout their life.

On the other hand, Darboux considers that the intestinal epithelium carries out the function of absorption. Also, Sellier's work seems to suggest that the wall of the intestine is an organ for the storage of digested substances.

Jordan does not figure any cells like the oldest excretion cells of Darboux (fig. 55, IX and X), though these form a most striking feature of all preparations (Pl. VI, fig. 54, *I.*). I am unable to find any cells which seem to link up the typical eosinophilous or globule-bearing elements with vacuolated cells casting off their tips. Cells (Jordan, S_6) which combine these two characters, if present at all, must be extremely rare.

It seems difficult, from histology alone, to controvert the views of Darboux. It is sufficient to state that secretion and absorption undoubtedly take place in the caeca and excretion also. Possibly this excretion is accomplished by secretory cells and actually accompanies the digestive ferment, or, these two types of cells may be different throughout their life.

III. *The Rectum.*

Posterior to the last pair of caeca the canal is differentiated as the Rectum. The epithelium (Pl. VII, fig. 56, *Ce.*) projects as a series of longitudinal ridges formed of elongated cells bearing long cilia. The nuclei are situated towards the ciliated border. The rectum terminates in the anus, which is bounded by an infolding of the body wall.

Summary of the Physiology of the Alimentary Canal.

The pharyngeal region of the digestive system is concerned with mechanical reduction of food and its admixture with secretions of abundant epithelial gland cells. The pharynx acts as a press. Posteriorly the lumen of the oesophagus is reduced to a narrow cavity and the adjacent anterior portion of the intestine forms an effective sieve by folding of its walls. Only finely-divided particles can pass through this apparatus and reach the intestinal lumen. The food undergoes partial digestion in the intestine. After a considerable lapse of time the anus is closed and the now fluid food is forced into the caeca. The little sieves at the bases of these organs filter out all but the very finest particles, so that nothing injurious passes into the delicate dorsal and ventral sacs. The brown fluid which fills the caeca consists of both nutritive and waste products. It contains finely disseminated food particles and numerous spherules (Pl. VII, fig. 55, XII), many of which bear large masses of yellow-brown granules. The position of the caeca is noteworthy, their delicate walls are closely apposed to the thin integuments of the dorsal tubercles and elytrophores; and the coelomic space separating them is occupied by blood vessels (Pl. V, fig. 38) and the perivisceral fluid.

The intestinal region of the canal plays an accessory rôle as an organ of defence. The contents of the caeca can be ejected from the anus and in this way an obscuring cloud is formed round the animal. It is probable that the " smoke screen effect " is accompanied by deterrent chemical activity.

Most narcotising fluids cause the worm to evacuate the contents of the caeca. In dissections this is a distinct advantage, as it prevents the discolouration of the organs which results when the brown fluid escapes through punctures in the thin walls of the caeca.

MUSCULATURE.

If Aphrodite be observed either in normal motion or when artificially stimulated, it is evident that the worm possesses a well-developed and wonderfully co-ordinated system of muscles, though its movements are somewhat slow. The action of some of the muscles lying close to the ventral body wall can be seen through the skin when the animal is induced to contract or partially to roll up.

In a typical Polychaet the musculature of the body wall is made up of a layer of circular muscle fibres in contact with the epidermis and an inner coat of longitudinal fibres.

The body wall muscles of the sea mouse differ considerably from this arrangement. The circular fibres are transformed into the two paired series of lattice-like muscles which are described below; they are situated dorsally and ventrally on either side of the middle line. The longitudinal muscles are well developed on the ventral surface, but dorsally they are rudimentary and thus almost the whole dorsal body wall consists of little but epidermal tissues lined by peritoneum. The longitudinal muscle coat of the body wall consists of four main bands running from the anterior to posterior end of the body. The paired dorsal longitudinal muscles are closely attached to the body wall on either side of the middle line. They are band-like and are separated from one another by a very narrow strip (Pl. VIII, fig. 67, *Dlm.*). They arise in the peristomium.

The paired ventral longitudinal muscles are separated medially by a considerable interval in which the nerve cord (Pl. IV, fig. 32, *Nc.*) lies. They arise in the first segment by several branches which fuse to form a pair of cylindrical muscles, and soon become broad flattened bands, each of which is firmly applied to the epidermal tissues by a median strip (Pl. VIII, fig. 67, *Vm.*).

In addition to these muscles there are the lateral longitudinal muscles (Pl. VIII, figs. 67 and 69, *Llm.*). They are discontinuous, being interrupted at the intersegmental intervals. They form a pair of bands which lie in the space marking the outer sides of the elytrophores (or dorsal tubercles) off from the notopodia.

The motor muscles of the pharynx have already been mentioned in connection with the eversion of this organ (see p. 42). If the musculature of the head and peristomium be excluded, the rest of the muscular system may be readily described. It exhibits a marked segmental arrangement, in which the lattice-like series play an important part.

The muscles which move the neuropodia backwards and forwards lie against the ventral body wall on the outer sides of the ventral longitudinal muscles. They constitute the ventral series of lattice-like fibres. In each segment two series of fibres arise from beneath the outer edges of the ventral longitudinal muscles. The fibres of the outer series (Pl. VIII, fig. 68, *Av.*) lie against the body wall.

They arise in the anterior half of the segment and converge as they pass forwards and outwards to their insertion at the base of the neuropodium at the anterior limit of the preceding segment. The second group of fibres, lying within the first, forms the inner series (Pl. VIII, fig. 68, *Pv.*). This series consists of a number of separate strands of fibres which arise from beneath the whole extent of the ventral longitudinal muscle in each segment. They pass backwards and outwards and converge to their point of insertion into the base of the neuropodium at posterior limit of the segment in which they lie. The anterior strand in each group is large and cylindrical, the others are smaller and more band-like.

In fresh specimens these muscles are readily distinguishable through the ventral body wall.

The corresponding series of muscles situated dorsally is somewhat similarly arranged (Pl. VIII, fig. 69, *Oem.*), but owing to the paired pouches of the dorsal body wall it lies in the plane which cuts the dorsal tubercles (or elytrophores) off from the coelom. The two groups of fibres arise in the middle of each segment at the sides of the dorsal longitudinal muscle. The inner group passes backwards to the posterior limit of the segment and is inserted against the lateral longitudinal muscle, and the outer group, which lies against the body wall, passes forwards to a similar insertion at the anterior limit of the segment. These muscles serve to move the elytra backwards and forwards.

The chief muscles traversing the coelom are the oblique muscles so characteristic of Polychaets. A number of band-like muscles arise in the space between the ventral longitudinal muscles on either side of the nerve cord. They form several groups, all of which are inserted into the body wall in intersegmental spaces.

One group—the dorso-ventral muscles (Pl. VIII, fig. 67, *DVm.*) passes dorsally to the outer sides of the dorsal longitudinal muscles at the posterior limit of the segment. The right and left members of this group cut off the median coelomic space in which the alimentary canal lies.

The remaining strands form the inferior oblique muscles. There are two groups. The ventral series is inserted into the base of the neuropodium at the posterior limit of the segment (Pl. VIII, fig. 67, *Iov.*) and the dorsal group (*Iod.*) passes anteriorly and is inserted into the notopodium and the base of the dorsal tubercle (or elytrophore). The inferior oblique muscles cut off the ventro-lateral compartments of the coelom in which the segmental organs lie.

In the centre of each segment a pair of stout muscles connect the inner or median border of the elytrophore (or dorsal tubercle) to the ventral body wall at the base of the neuropodium (Pl. VIII, fig. 69, *Iem.*). These are termed the Inner Elytrophore muscles.

Musculature of the Parapodia (Pl. VIII, figs. 70 and 71). The cavities of the parapodia are occupied by systems of muscles which move the feet and the setae. As the arrangement is similar in the two rami, it will be sufficient to describe the neuropodium.

The aciculum is a stiff rod, one extremity of which is embedded in the tissues of the tip of the foot and the other, the head, projects freely into the coelom. The heads of the acicula are capped by muscular pads from which numbers of band-like muscles radiate out in such a way that they form cones, the bases of which may be considered as lying in a plane cutting the parapodia off from the body. The muscles are inserted into the body wall at its intersection with this plane (fig. 70, *Prs.*). These muscles are the protractors of the whole foot and of its separate groups of setae.

The setal protractors (fig. 71) have an interesting grouping. The sac which encloses the setae is thickened in places to form little muscular caps containing the heads of several setae together. These caps are connected to one another and to the muscular bulb of the aciculum by bands of muscles.

The retractor muscles of the foot are attached to the head of the aciculum and are inserted into the body wall at the base of this rod. The retractor muscles of the setae are similarly situated. Co-ordination of the movement of the notopodia and neuropodia is brought about by stout muscles which connect the heads of their respective aciculi.

REPRODUCTION.

In regard to the formation of the reproductive bodies Aphrodite presents an example of one of the least specialised types found amongst the Polychaets. It is closely related to the condition met with in Nereis, in contrast to the development of definite sexual organs in forms such as the Arenicolidae. The majority of the marine worms are dioecious. Externally the sexes are often indistinguishable throughout life, but some forms exhibit vivid colour differentiation at maturity.

The sex cells always develop in connection with the coelomic epithelium, but the form and position of the proliferating areas vary greatly in different groups. In rare examples the germ cells arise from the epithelium of the floor of the coelom. More generally they develop from the septa or the peritoneal sheaths of the blood vessels. Sometimes the walls of special gonidial vessels, in connection with the nephridia, proliferate definite ovaries or testes, as in Arenicola, in which six pairs of sex glands are differentiated early in life; they can already be recognised in post-larval stages.

The condition, as met with in Aphrodite, is much less specialised. The sex cells are found on all the blood vessels except the dorsal and ventral vessels and the proximal portions of their lateral branches lying immediately above or below the alimentary canal (Pl. IV, fig. 32, left side). It is sometimes possible to pick out the mature females by the masses of cream-coloured eggs which can be distinguished through the thin walls of the parapodia. In specimens from Plymouth, mature males and females are common in October, when the males have been observed extruding sperm. Mature individuals from the same locality have been collected in March (records are not available over the whole year). Cuénot (9) records ripe males and females in May, and says that the extrusion of the sex cells occurs in June. The author has noted well-developed ova in specimens at Naples, during September.

Female. In mature specimens the coelom is filled with eggs which ooze out immediately the body wall is punctured. The sexual products pass to the exterior by way of nephridia; the nephridiopores are dorsally directed. In Polynoe the eggs are passed beneath the elytra, which then act as incubatory chambers. This is stated to occur also in Aphrodite (Haswell), but though the author has examined many mature specimens, eggs have not, so far, been seen in this position. Macroscopically, and also in sections, both eggs and sperms are readily distinguishable in the nephridial tubes.

The ova are differentiated from the peritoneal sheath of the blood vessels. In mature individuals the vessels resemble ropes of tiny pearls arranged all round the circumference of the thread (Pl. VII, fig. 57). They form beautiful dense meshworks (Pl. VII, fig. 58) which enclose the nephridia, the caeca and the intersegmental septa, and obscure the rest of the organs in the coelom.

The development of the ova has been described by Selenka (37), Cuénot (9) and others.

An early stage is represented in Plate VII, fig. 59. The peritoneal walls of the blood vessels bear scattered masses of regular cells* with densely granular cytoplasm and oval nuclei. Some of the cells of each group develop at the expense of their neighbours. These special cells, destined to become ova, are separated from one another by the undifferentiated elements which are acting as nurse cells. As the young egg cell matures, the nurse cells become irregular and flattened and, finally, some of them give rise to a thin membrane, or ovisac, enclosing each egg (Pl. VII, fig. 60, *O.Sac.*). The mature ova have large nuclei and definite nucleoli. A rich supply of yolk in the form of yellow oily globules fills the cytoplasm. The gradual accumulation of yolk is demonstrated by an alteration of the staining properties of the eggs. The cytoplasm of very young ova stains a deep bluish purple with haematoxlyin-eosin. As the cell grows, it exhibits an increasing affinity for eosin, so that fully mature ova stain a deep red.

The ova are freed into the coelom by rupturing the ovisac or by simply breaking through its stalk so that, when separated, they remain enclosed in the ovisac. In any sample the numbers of free and " ensacced " eggs are approximately equal. The empty ovisacs remain attached to the blood vessel (Pl. VII, fig. 57, *O.Sac.*) for some time.

Male. The body cavity of mature male specimens is filled with a milky fluid which can be recognised issuing from the nephridial apertures. On opening up such a specimen the spermatic fluid escapes and rapidly becomes flocculent owing to the aggregation of the sperms. The blood vessels have a transparent gelatinous appearance which makes them visible but individually indistinct.

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* Cuénot regards these masses as specialised lymph glands. He denies that they develop from the sheaths of the blood vessels but says they arise from cells of the septa. The author's investigations, however, agree with Selenka.

The developing male sex cells have the same distribution as the eggs in the female. The earliest stages of development are similar in the two sexes. The cells and the peritoneum ensheathing the blood vessels divide and give rise to groups of cells (Pl. VII, fig. 59) of uniform appearance. In the male these cells are succeeded by large cells of characteristic form which may be termed the primary spermatogonia (Pl. VII, fig. 61*a* and *b*, *Sg.*). These spermatogonia have large oval nuclei in various stages of mitosis and often conspicuous nucleoli. They lie adjacent to the endothelium lining the blood vessels. By division they give rise to numerous generations of spermatogonia. In many sections of "mature" vessels a rough zonal arrangement of the cells can be made out. The primary spermatogonia give rise to smaller cells which divide rapidly to form irregular groups of cells (Pl. VII, fig. 61*b*, *f.*) which are similar in character. The cell wall is indistinct, the nucleus is enclosed by a definite membrane and contains a conspicuous nucleolus, but the cell is otherwise not remarkable.

The cells of the next zone are slightly smaller but striking. They occur as masses of closely packed elements with intensely staining nuclei (Pl. VII, figs. 61*a* and *b*, *g.*) of very uniform appearance. They are aggregated into irregular lobules and this gives rise to the raggedness of "mature" vessels.

The succession of cells just described cannot be demonstrated throughout the period of the growth of the sex cells. Often the smaller spermatogonia (Pl. VII, fig. 61*b*, *f.*) are absent (fig. 61*a*), or the different types of cells may be irregularly scattered.

Further development takes place in the coelom. The lobules (Pl. VII, fig. 61*a*, *g*.) break up and the cells are cast into the coelomic fluid, either singly or in groups. The details of the meiotic phase have not been worked out and it is not decided whether these deeply-staining cells are the last generation of spermatogonia, which have already become primary spermatocytes whilst attached to the blood vessel, or whether further division takes place in the coelomic fluid before the characteristic two divisions give rise to the spermatids.

From the apparent absence of anything corresponding to a typical spermatophore it seems probable that they are the primary spermatocytes. In the coelomic fluid of mature specimens, besides active spermatozoa (Pl. VII fig. 61, *d*.), groups or single examples of these cells occur. Also, sperms attached in groups of four are common, and similarly arranged tailless spermatids (Pl. VII, fig. 61*c*, *St*.).

NEPHRIDIA.

The nephridia are situated ventro-laterally in the compartments of the coelom cut off by the inferior oblique muscles (Pl. V, fig. 38, *Nph*.). Typically there are 15 pairs lying in segments XI to XXV, inclusive, but the number is not absolutely constant; specimens are met with in which 14, 16 or 17 pairs are present.

They are readily exposed by severing the necks of the caeca and removing the alimentary canal and then cutting through the attachments of the oblique muscles at the median sides of ventral longitudinal muscles (Pl. VIII, fig. 67, *Cut*.).

The nephridia will now be recognised as little yellow tubes coiling round the inner sides of the muscles of the neuropodial setae.

Nephridia are developed from the ectoderm of the embryo. They are essentially simple canals leading from the coelom to the exterior. Their function is excretory. The coelomic opening of the canal is termed the nephrostome and the external aperture is known as the nephridiophore. The nephridiopores of Aphrodite have already been seen at the tips of the nephridial papillae (see p. 19).

In the Aphroditidae a so-called " nephridium " is a compound organ consisting of the nephridium proper and a ciliated funnel with which it is fused. Ciliated funnels are essentially genital ducts. In some groups of worms the genital ducts and nephridia remain separate throughout life, but in a great many cases the genital ducts, with their wide internal orifices forming the ciliated funnels, come into relationship with the nephridial tubes. This union may be temporary, during the reproductive period only, or permanent, as in Aphrodite, Hesione, Arenicola and many others. The relations of these two structures in the Polychaeta have been worked out by Goodrich (22, 23, 34).

The following description of the course of the nephridium in Aphrodite commences at the nephridiopore. The first part of the canal is an invagination of the tip of the nephridial papillae (Pl. VII, fig. 64) ; the tube proper commences at the level of the body. It is of narrow diameter and runs ventrally and slightly anteriorly until it reaches the outer series of muscles (Pl. VIII, fig. 68, *Av.*) lying against the body wall ; it passes beneath these muscles and expands into a broad sac. The tube then bends dorsally and runs inwards, continuing to pass forwards beneath the neuropodial setal muscles, round which it curves dorsally and eventually reaches the anterior limit of the segment in which it lies. As it passes into the preceding segment the tube expands to form a wide-mouthed funnel (Pl. VIII, fig. 65, *Cil.f.*) which lies against the anterior face of the septum (Pl. VIII, fig. 66, *Cil.f.*). The whole of the posterior portion of the tube is distinctly yellow in colour, but as the septum is approached its walls become white and transparent.

The opening of the organ into the coelom (fig. 65) is, morphologically, a combination of a nephrostome and a genital funnel. It is bounded by two lips situated dorsally and ventrally, which form the ciliated funnel. The ventral lip (Pl. VIII, figs. 65 and 66, *Vl.*) is a rounded deflection of the rim of the orifice and lies against the septum. The dorsal lip has the form of a remarkably beautiful fluted petal with extended lateral margins. Its pearl-like transparency during life suggests the delicate shell of Argonauta.

The inner surface which faces forwards is striated with fine ciliated grooves which radiate outwards and fade away towards the margins of the funnel, where it lies against the septum. The projecting lateral edges of the lip pass forwards and downwards and lie close to the ventral body wall. The funnel wraps round the muscles which support it and, therefore, when removed entire, it is impressed with a number of folds (Pl. VIII, fig. 66).

The yellow, or excretory, portion of the tube is also marked by striations due to longitudinal folds, which are most definite towards the nephridiopore. The lumen of the tube, like the funnel, is clothed by a dense coat of cilia. During life each groove is a channel leading to the cavity of the nephridium, down which bodies floating in the coelomic fluid are wafted by constantly waving cilia. The coelomic fluid is kept in continual motion by the activity of the peritoneal cilia, sex cells and other solid bodies are thus readily brought into contact with the funnel and so passed to the exterior.

In mature males the nephridia are often so packed with sperms that the yellow colour of their walls is obscured by the dense white contents, which give the organs quite a solid appearance.

The wall of the nephridium consists of a single layer of yellow ciliated cells clothed by the coelomic epithelium. It may be regarded as a membrane capable of extracting certain substances from the coelomic fluid. These waste products are collected by the yellow cells and passed into the lumen. The yellow or excretory cells (Pl. VII, fig. 62) are very delicate, their walls are only distinct towards the ciliated surface. The basal portions of the cells form a syncytium of vacuolated protoplasm containing masses of yellow excretion granules (*Eg.*) and well-defined oval nuclei. The cilia are long and evenly distributed, they are continuous with rows of granules which extend half-way through the depth of the cells.

The epithelium of the funnel (Pl. VII, fig. 63) is thrown into a number of deep folds. Cell walls appear to be absent, the protoplasm is granular, the nuclei are oval and the cilia are evenly distributed. The basement membrane is folded together with the epithelium which rests on it. The coelomic surface of the funnel is clothed by the peritoneum which, not being folded, encloses longitudinal spaces corresponding to the ridges of the folds. These ridges fade away towards the edges of the lip ; therefore, here the ciliated epithelium of the funnel lies flat on the peritoneum.

The nephridia of Aphrodite are somewhat similar to those of Hesione (22). The chief difference lies in the radial ridging of the funnel of the former as compared with parallel folding of the latter. They more closely resemble the description given by Storch (62) for *Hermodice caruncalata*, the difference being that in this form there is much less inequality of size between the two lips. The nephridium of *A. aculeata* figured by Fage (19) appears to be fragmentary.

NERVOUS SYSTEM.

The nervous system is constructed on the typical Annelid plan. It consists of a mass of nerve tissue situated in the prostomium, connected by a ring encircling the alimentary canal with a chain of ganglia lying along the middle line of the ventral body wall. The paired nerves which form the ring are termed the Oesophageal Connectives (Pl. VIII, fig. 72, *Oes.C.*) and the ganglion situated at their point of union in the fourth segment is termed the Sub-oesophageal Ganglion (Pl. VIII, fig. 72, *Oes.G.*). The remaining ganglia, termed Ventral Ganglia (*VG.*), are connected to one another by a distinctly double nerve cord. The so-called oesophageal nerve ring is sufficiently wide to permit the pharynx to pass through, and when this takes place the ring is really peri-pharyngeal. In Aphrodite it never becomes truly peri-oesophageal owing to the limited eversibility of the pharynx.

During life the whole of the central nervous system is bright red in colour and so it can be readily seen through the integument (Pl. II, fig. 2, *Nc.*), but the colour is rapidly destroyed by preservatives. Ray Lankester (41) has proved this rather unusual colouration to be due to the presence of haemaglobin.

The nerve mass of the prostomium which supplies nerves to the prostomial sense organs is often termed the " brain " or the " supra oesophageal ganglion." The former term is inaccurate as it suggests a comparison with the vertebrate brain, and the latter is not much better because it suggests that this anterior ganglionic mass is homologous with one of the ventral ganglia. It is, however, probable that this nerve mass is the chief centre and, through the medium of the oesophageal connectives, it may be regarded as presiding over the activities of the ganglia of the ventral chain.

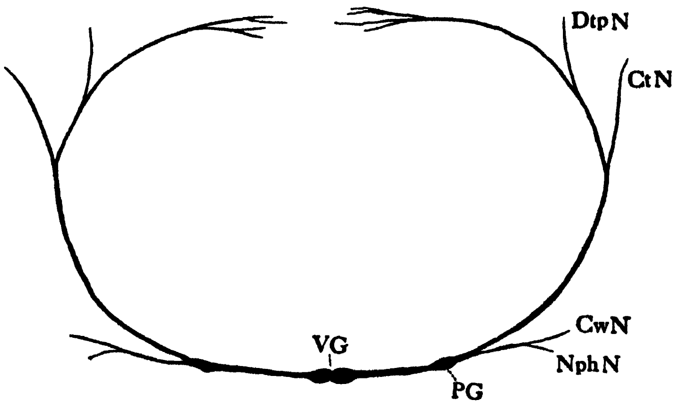
In the following discussion the term "Cephalic Nerve Centre" will be employed to signify the whole of the nerve tissue situated in the prostomium.

Each of the oesophageal connectives arises from the cephalic nerve centre by two short rami which fuse and swell out to form a pair of large masses—the Commissural Ganglia (Pl. VIII, fig. 72, and Pl. X, fig. 82, *Com.G.*) lying just posterior and ventral to the base of each palp. The course of the connectives is readily seen by cutting through the dorsal and ventral motor muscles of the buccal mass on one side and deflecting the alimentary canal to the opposite side.

The first ventral ganglion is so closely apposed to the sub-oesophageal ganglion that it appears to be part of the latter, but on careful examination and, from sections, a very short segment of the double nerve cord can be seen to connect them. This ganglion (Pl. VIII, fig. 72, *VG.* 1) supplies the fifth trunk segment (*PN.* 5). Altogether there are 39 ventral ganglia. The second is close to the first but those in the central region of the body are more widely separated. At the posterior extremity where the segments are very small, the intervals between the ganglia are practically absent.

Each typical segment is innervated by three pairs of nerves which pass out laterally from its ventral ganglion. All the lateral nerves pass beneath the ventral longitudinal muscles, on the median side of which they lie freely in the coelom, but on the distal side the two anterior pairs of nerves pass immediately into the sub-epithelial connective tissue, where they branch to form a complete peripheral network lying in the epithelium. The posterior pair of lateral nerves are the largest and are distinguished as the Podial Nerves (Pl. VIII, fig. 72, *PN.*). They supply the special parapodial organs and the dorsal body wall.

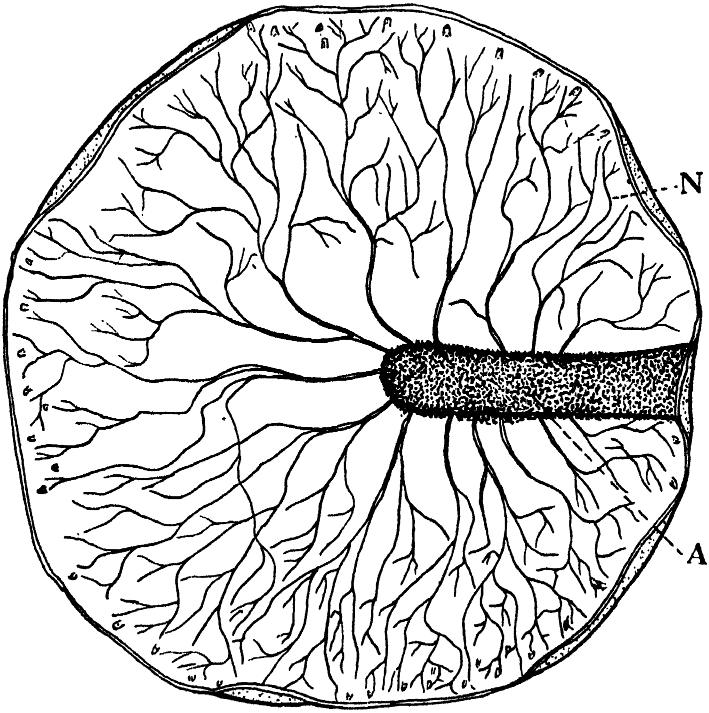
The podial nerves have the same distribution in each segment (Text-fig. 13). Each passes slightly posteriorly beneath the ventral longitudinal muscles to a small podial ganglion (*PG.*) lying at the base of the neuropodium. From the ganglion two branches arise. One runs along the ventral wall of the neuropodium and sends a branch to the nephridium (*Nph.N.*) and then terminates in the neurocirrus (*Cw.N.*). The other and main branch continues its course upwards till it reaches the dorsal body wall. It gives off a nerve to the notocirrus (*Ct.N.*) and another to the dorsal fimbriated papilla (*Dtp.N.*) (or to the elytron). In the dorsal and lateral wall it breaks up into a number of branches which form a complete network lying in the epithelium. This peripheral nerve network can be readily made out in pieces of tissue stained with haematoxylin (Pl. III, fig. 15). The nerve plexus of the elytron can be demonstrated in the same manner (Text-fig. 14). The larger branches of the nerves are rendered distinct because the slightly wavy nerve fibres stain much more deeply than the surrounding sheath. The plexus is so complete that its branches come into relation with almost every individual cell of the integument. A similar



TEXT-FIG. 13. Diagram illustrating course of a podial nerve.

network has been demonstrated by Jourdan (35) in *Hermione hystrix.*

The four anterior podial nerves are concentrated by the presence of the oesophageal nerve ring. The right and left members of the first pair (Pl. VIII, fig. 72, *PN*.1) arise from the corresponding commissural ganglion (*Com.G.*), from each of which a nerve also passes to the facial tubercle (*Fi.*). The podial nerves of Segments II, III and IV arise from the sub-oesophageal ganglion and pass forwards with the oesophageal connectives to which their bases are united by a common sheath (Pl. X, fig. 86). They therefore appear to arise from the oesophageal



TEXT-FIG. 14.

commissures but, in reality, no nerves are given off in this manner.

The nerve cord of the Hermioniae differs from that of the Polynoids and Sigalions in several characters. In the Polynoids and Sigalions it is band-like, the ganglia are ill defined and the whole chain lies within the epidermal tissues. In the Hermioniae, of which Aphrodite is a good example, the ganglia are distinct and the cord lies freely in the coelom. The ventral cord and its branches are surrounded by a neuroglia sheath and it is only connected to the ventral body wall by a fold of peritoneum.

STOMATO-GASTRIC NERVOUS SYSTEM.

The nerve supply of the digestive system lies completely within the epithelium of the alimentary canal. It arises in the cephalic nerve centre by a pair of nerves (Pl. VIII, fig. 72, *Lbm.*) which issue from the prostomium close to the commissural ganglia. In fresh specimens these lateral buccal nerves can be readily seen running in the wall of the buccal mass. (Cut the dorsal motor muscles through on one side.) The rest of the system is best examined by removing the pharyngeal region from the coelom and slitting it up along the mid-dorsal line (Text-fig. 10, *Nsg.*).

At the junction of the buccal mass with the pharynx, the lateral buccal nerves terminate in a pair of ganglia (Pl. VIII, fig. 73, *Lbg.*) from which the main nerves of the system are distributed. They may be termed the Lateral Buccal Ganglia; they are connected by two rings, one of which lies in the epithelium of the papilla cushion (*AR.*) and the other (*PR.*) is situated posterior to it at the base of the jaws. The anterior ring gives off nerves to the pharyngeal papillae and forms a dense network in the epithelium of this region. The posterior ring also gives off numerous branches. Each of the four main longitudinal nerves of the pharynx (Text-fig. 10, *Nsg.*) is formed by the fusion of two nerves, one of which arises from the lateral ganglion and the other from the middle of the posterior ring (Pl. VIII, fig. 73, *Stg.*). Posteriorly the longitudinal nerves divide into many branches (Pl. VI, fig. 48, *Nsg.*) which supply the oesophagus and intestine.

THE CEPHALIC NERVE CENTRE.

The cephalic nerve centre, when removed from the prostomium, is a roughly trapezoidal mass. An indication of bilobed structure is given by a narrow median groove which occupies the dorsal surface and continues round the posterior end and along the ventral surface as a deep U-shaped furrow which fades away anteriorly. The postero-lateral areas of the ventral surface are swollen into a pair of rounded bosses from which the Commissural Ganglia and the bases of the Stomato-gastric nerves project.

The prostomial nerve mass of the Aphroditidae has been studied by Rohde (54, 55), Haller (26), Pruvot (49), Racovitza (53), Darboux (15) and others. Rohde (55) and Haller paid particular attention to the histological nature of the nervous system, whilst the works of Racovitza and Darboux deal chiefly with the relationship of the various parts. Racovitza (53), in an extensive research, surveyed the whole literature of the Polychaet " brain " and added much that was new. In order to describe satisfactorily the prostomium of *A. aculeata*, it is necessary to give here a brief abstract of this author's important and interesting discussion.

Racovitza used the term " *Encephale* " to signify the whole of the nerve mass lying in the prostomium. In the description to follow this term, so defined, is rendered as Cephalic Nerve Centre.

According to Racovitza the primitive Polychaet *encephale* may be regarded as consisting of three separate nerve masses, each of which is in direct contact with the epidermis of the prostomium. He termed the three masses " *cerveaux anterieur,*" " *cerveaux posterieur* " and " *cerveaux moyen,*" the terms indicating the relative positions of the nerve masses in the primitive condition. (In the absence of a more suitable terminology these names are, respectively, translated as anterior lobule, posterior lobule and mid-lobule.)

The three surfaces of contact of the primary lobules (*b.*) with the epidermis are primitive sensory areas (*a.*) with special functions, explained by the following table :—

		Sense Organs	Function
I. Palpary region ...	Consisting of :—		
	a. Palpary area ...	Gustative fosettes	Tactile and gustative
	b. Anterior lobule	Palpary nucleus	
II. Sincipital region ...	Consisting of :—		
	a. Sincipital area	Eyes Tentacles	Visual and tactile
	b. Mid lobule ...	Optic nuclei Tentacular nuclei	
III. Nucal region	Consisting of :—		
	a. Nucal area ...	Nucal organ	Olfactory
	b. Posterior lobule	Nucal nuclei	

The actual organs of sense are specialised portions of the original sensory areas, usually in the form of projections, the epidermis of which retains contact with its lobule by means of nerves. The nerves are reinforced by fibres from groups of nerve cells forming special "nuclei" (= ganglia of Racovitza). The degree of development of nerves and nuclei is thus closely correlated with that of the prostomial sense organs. For example, Polychaeta with well-developed eyes have large optic nuclei associated with the mid-lobule, whilst those, like *A. aculeata,* in which the palps are the chief prostomial organs, possess large palpary nuclei associated with the anterior lobule.

All previous workers agree that two of these three primitive lobules are present in the Aphroditidae. Rohde calls them the dorsal and ventral ganglia. Racovitza and Darboux term them the "cerveaux moyen" and "cerveaux anterieur." Pruvot and Racovitza (49*a*), in a joint work, stated that some Sigalionidae possess a nucal organ, but Darboux proved this to be an error. Racovitza (53) did not work on Aphroditidae, but stated that the nucal organ was present in some. Darboux was unable to find either a nucal organ or its associated lobule in any member of this family. Both are definitely absent in *A. aculeata*.

Applying Rocovitza's scheme, invented for the analysis of the Polychaet *encephale*, to the condition in Aphrodite, we have drawn up the following plan :—

I. Palpary region of prostomium	Palpary area of epidermis	Consists of 1 pair massive palps.		
	Innervated by anterior lobule of cephalic centre.	" "	Nerve cells and mass of fibres.	Palpary nuclei with nerves to palps, and other nerve cells surrounding the fibre mass. Ant. rami of Oes. Connectives and stomatogastric rami.
II. Sincipital region of prostomium	Sincipital area of epidermis.	" "	1 pair non-pedunculated eyes and 1 tentacle.	
	Innervated by mid lobule.	" "	Nerve cells and mass of fibres.	No differentiated nuclei. Cells surround fibre mass and bases of nerves leaving it. Optic nerves; tentacular nerve; Post. rami of Oes. Connectives.
III. Nucal region of prostomium	Nucal area of epidermis innervated by posterior lobule.	absent in Aphrodite.		

Jourdan (36) first clearly stated the fact that the cephalic centre is entirely ectodermal in origin. This is supported by embryological evidence. Kleinenberg (39) demonstrated the growth of the prostomial nerve mass in Phyllodoce and Lopodarhynchus from three originally distinct ectodermal thickenings. Racovitza (53) extended this view by a detailed study of the Nucal Organ of numerous Polychaets. He concluded that the sense organs and lobules represent respectively, the cuticular and basal portions of the original epidermis of the primitive sensory areas. In several regions these two portions become separated and the coelomic cavity is interposed between them. The cavity of the head is continuous with the cavity of the peristomium. It is very much reduced and is almost wholly occupied by nervous tissue and muscles. The nervous tissue is entirely contained between the cuticle and basement membrane. It may be regarded as thickenings of this region retaining connection with the external surface at certain definite points.

In Aphrodite three canal-like projections of the coelom occur dorsally. One of these is median and runs forwards to the cavity of the ceratophore (median tentacle) (Pl. IX, figs. 76 to 78, Pl. X, figs. 79 and 80, *M.coe.*). It lies directly beneath the epidermis. The other two are paired ; they extend from the posterior coelomic cavity as two diverging and widening canals which pass forwards and end blindly just anterior to the eyes (Pl. IX, figs. 76 to 78, Pl. X, figs. 79 and 81, *L.coe.*). For the greater part of their course they run through the connective tissue (*Nlg.*) of the cephalic centre, but anteriorly they lie close to the epidermis. They serve to distribute coelomic fluid to the head.

The whole of the nervous system is protected by a well-developed sheath which ceases only at the terminal twigs of its peripheral branches. In the prostomium the sheath is so thick that it might well be described as a capsule enclosing the nervous elements. (In Plates IX and X the capsule is represented by the sparsely-dotted area.) It is made up of a connective tissue termed neuroglia (Pl. X, fig. 83, *Nlg.*). According to Rohde (54) and others this tissue is due to an exaggeration of the fibrillar structure of sub-epidermal cells. Its fibres are in contact with the supporting cells of the epidermis. It consists of a finely granular matrix, with irregular dense patches, traversed by a network of fine anastomosing fibres (*Ngf.*). In some planes the fibres have a distinctly parallel arrangement. Neuroglial nuclei are absent, but groups of highly refractive yellowish granules occur at irregular intervals and some of these appear to surround a nucleus (Pl. X, fig. 83, *AcN.*) while others do not (*Acg.*). They represent wandering or Amoeboid cells in process of degeneration (Racovitza (52)). They are present in another form as small deeply-staining granular elements (*Ac.*) with well-marked nuclei.

The nervous tissue of the cephalic centre, exclusive of the neuroglia capsule, consists of a ganglion cell cortex and a central mass of fibres so characteristic of invertebrate ganglia. This latter is the well-known Punkt-substanz of Continental workers ; it is formed of the processes of the ganglion cells lying in the neuroglia. The punkt-substanz appears finely granular or finely striated, according to the way in which its fibres are cut. For convenience the term " punkt-substanz " is retained.

The cephalic centre (Pl. IX, figs. 76 to 78, and Pl. X, figs. 80 to 82) is divisible into a middle dorsal mass, the Mid-lobule (*Mb.*) and a ventral anteriorly projecting mass which constitutes the Anterior lobule (*Ab.*). The posterior lobule, as previously explained, is absent. Peripherally the two lobules are distinct, but the central punkt-substanz is undivided.

Just posterior and lateral to the eyes a pair of large, approximately ovoidal, masses of closely-packed ganglion cells form the Palpary nuclei (*Pg.*) from each of which a thick stalk of fibres passes to the anterior lobule. These structures form a striking feature of both transverse (Pl. IX) and longitudinal sections (Pl. X, fig. 82, *Pg.*).

The ganglion cells constituting the cortex are symmetrically arranged round the central mass of nerve fibres and they encircle the bases of the nerves which arise from it. There are three chief types of ganglion cells.

Type I. Large, pear-shaped cells (Pl. X, fig. 83, *Uc.*) embedded in the neuroglia capsule and sending a single process to the central mass of fibres. The nuclei of these cells stain deeply, they are rich in chromatin and have distinct nucleoli and well-defined nuclear membranes. The perinuclear area of cytoplasm is densely granular, but towards the cell wall it is vacuolated; thus sections through this peripheral area appear as round, almost empty spaces.

Type II. Smaller ganglion cells with rounded nuclei and dense cytoplasm occur between the unipolar nerve cells (Type I) and form sheaths round the bases of the nerves supplying the sense organs.

Type III. Nerve cells of the palpary nuclei (Pl. IX, fig. 74, *N.Pg.*) are deeply staining and spherical, and they occupy almost the whole of the cell body. It is only possible to follow the cell processes for very short distances; they soon appear to fuse to form a tree-like system of fibres culminating in the stalk (Pl. X, fig. 82) already mentioned.

The *distribution of Fibres and Cells in the Cephalic Centre* is illustrated by transverse longitudinal sections of the prostomium (Pls. IX and X).

The *Mid-Lobule* (figs. 76 to 82) supplies nerves to the median tentacle and to the eyes. It also gives rise to one of the rami of the œsophageal connectives. It consists of an irregularly shaped central mass of fibres (*Mbf.*) surrounded by ganglion cells. Peripherally (figs. 76 to 81, *Mbf.*) the mid-lobule is distinct from the anterior lobule (*Abf.*), but in the centre the masses of nerve fibres are closely apposed (Pl. X, fig. 80).

The *Paired Optic Nerves* (Pl. IX, figs. 76 to 78, and

Pl. X, fig. 81, *ON.*) arise dorsally from the fibre mass of the mid-lobule. They are ensheathed by ganglion cells (type II) whose processes pass into the nerves. Owing to the non-pedunculated condition of the eyes, the optic nerves are very short.

The *Nerve of the Median Tentacle* (Pl. X, fig. 80, *AN.*) also arises from the dorsal region ; its base is surrounded by nerve cells of Type II.

Each *Oesophageal Connective* arises from the cephalic nerve centre by two roots, termed the Anterior and Posterior Rami, issuing respectively from the anterior lobule and the mid-lobule. The Posterior Rami (Pl. IX, figs. 77 and 78, and Pl. X, fig. 81, *RP.*) arise laterally from the mid-lobule. Each ramus passes ventrally round the inner sides of the base of the palp to the commisural ganglion (*Com.G.*)of its side.

The *Anterior Lobule* supplies the palps, the anterior rami of the oesophageal connectives and the stomatogastric nervous system. Its central mass of nerve fibres (Pl. X, fig. 80, *Abf.*), lying beneath the mid-lobule, gives off large lateral expansions (Pl. IX, fig. 77, *Abf.*) surrounded by nerve cells (Types I and II).

The *Paired Palpary Nuclei* (Pl. IX, figs. 76 to 78, and Pl. X, figs. 79 and 82, *Pg.*) are roughly mushroom-shaped. The "head" consists of a mass of multipolar ganglion cells (Type III) with three or four processes which join up to form the "stalk." Nerve fibres from the stalk either mingle with the fibres of the anterior lobule (*Abf.*) or pass directly to the anterior ramus of the oesophageal connectives (Pl. X, fig. 82, *RA.*) and to the Palpary nerve (*PpN.*).

The *Anterior Rami of the oesophageal connectives* (Pl. IX, fig. 81, and Pl. X, fig. 82, *RA.*) are formed by fibres issuing directly from the punkt-substanz of the anterior lobule and by fibres from the palpary nuclei. Each ramus passes backwards and outwards round the outer side of the base of the palp, beneath which it fuses with the posterior ramus of its side and enters the Commissural ganglion.

The *Palpary Nerves* (Pl. IX, figs. 76 and 77, and Pl. X, fig. 82, *PpN.*) are formed of fibres from the palpary nuclei, together with fibres arising directly from the anterior lobule.

The *Paired Stomato-gastric Nerves* (Pl. IX, fig. 77, and Pl. X, fig. 81, *RS.*) arise close to the middle line from the ventral region of the anterior lobule, in front of the anterior rami of the connectives. Each nerve passes backwards and outwards parallel to and on the inner side of the posterior rami of the oesophageal connectives and issues from the cephalic capsule close to the commissural ganglia.

A broad bundle of fibres (Pl. X, figs. 79 to 81, *Y.*), derived from the mid-lobule, runs through the neuroglia capsule to its posterior border. This nerve resembles a similar structure described by Haller (26) in *Nereis costi.* It also appears to be the posterior portion of a structure termed " Hirnhorner " by Rohde (55) in a description of the cephalic centre of *Polynoë elegans.*

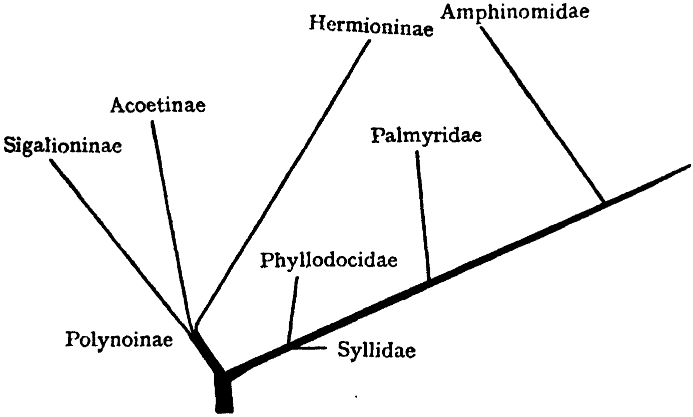
STRUCTURE OF VENTRAL CHAIN.

The majority of the nerve cells of the Ventral Ganglia are large unipolar pear-shaped cells belonging to Type I. Plate X, fig. 84, illustrates the distribution of ganglion cells in the sub-oesophageal ganglion. The cell bodies are embedded in the neuroglia and the processes pass into a central mass of fibres. In absolutely transverse sections there is a marked symmetry of arrangement of both the cells and the fibre tracts.

Plate X, fig. 85, illustrates a transverse section through one of the anterior ventral ganglia. It passes through the axis of a Giant Cell (Pl. IX, fig. 75). The neuroglia sheath is very well developed.

AFFINITY OF *A. ACULEATA*.

The possession of elytra unites the assemblage of genera forming the Aphroditidae into a family which is distinctly marked off from the rest of the Polychaets. The elytra-bearing worms are generally recognised as being more closely related to the Syllidae and Phyllodocidae than to any of the other families. The relations of the various groups are represented in the diagram below :—



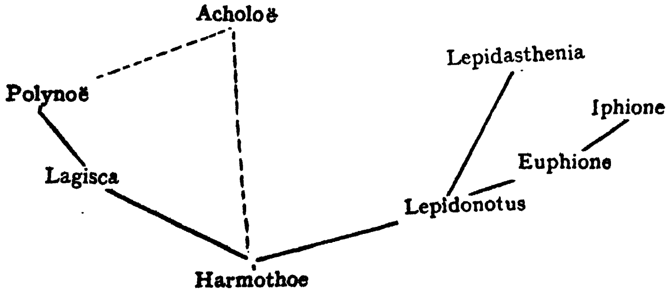
(From Darboux.)

Within the family Aphroditidae the Polynoinae approach the primitive type most clearly. The genera of this subfamily are varied in structure. They differ from one another in many important characters, the chief of which are body form and number and distribution of the prostomial tentacles. Their habitat is largely littoral, they are commensals, possibly some are parasites, living in company with tube-inhabiting Annelids and Echinoderms. They are also found in association with sponges, Coelenterates, Molluscs and Tunicates.

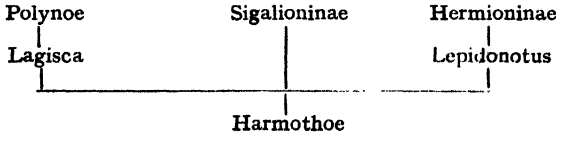
Harmothoe is generally regarded as the genus which most resembles the primitive Polynoid. It is found adhering to the inner walls of the tubes of various Annelids and is characterised by a short flattened body consisting of few segments.

Darboux (15) considers that a form resembling Harmothoe gave rise to two branches, one of which passes through forms represented by Lagisca and Polynoe, to the genus Acholoë. Acholoë and its allies have many segments and are vermiform. From the genus Acholoë the Sigalioninae are derived. Sigalions mostly live buried in coarse sand, without definite galleries. They possess well-developed branchiae.

The other branch culminates in Iphione. This genus is linked with Harmothoe, through the generic types Euphione and Lepidonotus. Iphione has a short flattened oval body consisting of few segments. The elytra are firmly fixed and completely cover the dorsum. Iphione represents the form from which the Hermioninae are derived. The characters of this sub-family are well represented by *Aphrodite aculeata.* The following table, taken from Darboux, represents the relationships of the Polynoinae to one another :—



It has been modified by Bohn (6) thus :—



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EXPLANATION OF PLATES.

REFERENCE LETTERS.

A. = Attachment area of elytron.
Ab. = Anterior lobule.
Abf. = Mass of fibres of anterior lobule.
Ac. = Wandering cell (Amoebocyte).
Acg. = Granules of wandering cell.
AcN. = Nucleus of wandering cell.
Ai. = Aciculum.
Ali.C. = Alimentary canal.
AN. = Nerve to Median tentacle.
An. = Anus.
AR. = Anterior ring of stomato-gastric Nervous System.
Av. = Outer series of muscles lying against ventral body wall.

Bc. = Coelom.
bg. = Yellow-brown granules in epithelium of caecum.
Bm. = Basement membrane.
Bv. = Blood vessel.

C. = Cuticle.
Cae. = Intestinal caecum.
C.c. = Cephalic nerve centre.
Cct. = Connective tissue corpuscle.
Ce. = Columnar epithelial cell.
Cil.F. = Ciliated funnel of Nephridium.
Cil.P. = Ciliated cells of Peritoneum.
Cmf. = Circular muscle fibres.
Cn. = Posterior part of muscle coat of Oesophagus.
Com.G. = Commissural ganglion.
Cs. = Cirrus.
Ct. = Notopodial cirrus.
Cts. = Connective tissue septum.
Cw. = Neuropodial cirrus.

Db. = Dorsal lip of ciliated funnel.
de. = Dorsal edge of facial tubercle.
Dlm. = Dorsal longitudinal muscle.
Dp. = Dorsal plexus of blood vessels.
Ds. = Dorsal sac.
Dtp. = Dorsal fimbriated papilla.
Dv. = Dorsal (blood) vessel.
DVm. = Dorso-ventral muscles.

e. = Endothelium of blood vessels.
Eb. = Elytron.
Ef. = Fibres of elytron.
Eg. = Excretion granules in cells of Nephridium.
eg. = Eosinophilous globules in cells of caecal epithelium.
Ex. = Encrustations on dorsal surface of elytron.
Eye. = Eye.
F. = Felt.
Fi. = Nerve to facial tubercle.
Fc. = Fibro-cells forming core of palp.
Ff. = Circular fibres at base of epidermis of palp.
Ft. = Facial tubercle.
Gc. = Gland cell.
Gd. = Duct of gland cell.
Ggs. = Giant nerve cell.
Gs. = Nerve cell.

Ht. = "Heart."
Ie. = Intestinal epithelium.
Iem. = Inner muscles of elytrophore.
Int. = Intestine.
IOd. = Inferior oblique muscles: dorsal group.
IOv. = Inferior oblique muscles: ventral group.
Ip. = Intra-epidermal pocket.
J. = Jaw.
K. = Cavity separating outer connective tissue sheath from muscles of jaws and papillae—anterior region of pharynx.
Kf. = Ceratophore.
Kt. = Ceratostyle.
Lbg. = Lateral buccal ganglion (Stomato-gastric Nervous System).
Lbm. = Lateral buccal nerve (Stomato-gastric Nervous System).
lc. = Lateral cushion (muscles between jaws).
L.coe. = Lateral coelomic canals (prostomium).
Li. = Inferior lip.
Llm. = Lateral longitudinal muscles (of body wall).
Lm. = Longitudinal muscles fibres.
Lp. = Lateral plexus of blood vessels (in intersegmental septum).

M. = Muscle.
Mb. = Mid-lobule.
Mbf. = Mass of nerve fibres of mid-lobule.
Mc. = Circular muscle fibres.
M.coe. = Median coelomic canal (prostomium).
Mes. = Mesentery.
Mm. = Motor muscles of pharynx.
Ms. = Muscles "amortisseurs."
Mth. = Mouth.

N. = Nerve.
Nc. = Ventral nerve cord.
Ncc. = Cirrophore.
Ncs. = Cirrostyle.
Ne. = Nucleus.
Ngf. = Fibres of neuroglia.
Ni. = Nuclei of syncytium of elytron.
Nk. = Neck of intestinal caecum.
Nlg. = Neuroglia.
NPg. = Ganglion cells of palpary nuclei.
Nph. = Nephridium.
Nsg. = Stomato-gastric nerves.
Nt. = Notopodium.
Nu. = Neuropodium.

O. = Ovum.
Oem. = Outer elytrophore muscles.
Oes. = Oesophagus.
Oes.C. = Oesophageal commissures.
Oes.G. = Sub-oesophageal ganglion.
ON. = Optic nerve.
O.sac. = Ovisac.
Ots. = Outer connective tissue sheath (Pharynx).

P. = Peritoneum.
Pap. = Papillae (epidermal).
Par. = Parapodium.
Pb. = Bases of pharyngeal papillae—cut across.
Pc. = Papilla cushion.
P.coe. = Coelom of prostomium.
PG. = Podial ganglion.
Pg. = Palpary nucleus.
Ph. = Pharynx.
Phs. = Buccal mass.
PN. = Podial nerve.
Pp. = Palp.
P.P. = Pharyngeal papillae.
PpN. = Palpary nerve.
PR. = Posterior ring (Stomato-gastric Nervous System).
Pro. = Prostomium.
Pns. = Basal processes of epidermal cells.
Prs. = Protractor muscles of setae and aciculi (figs. 70 and 71).
Pv. = Inner series of muscles lying against ventral body wall.
Pr. = Processes of epidermal cells.

RA. = Anterior ramus of oes. connective.
Rmf. = Radial muscle fibres.
RP. = Posterior ramus of oes. connective.
RS. = Ramus of stomato-gastric Nervous System.

S. = Setae.
Sa. = Sieve.
Sb. = Muscles forming a shining band at anterior end of pharynx.
Sc. = Epithelial cell of cirrostyle.
Sep. = Sub-cephalic plate.
Sept. = Intersegmental septum.
Sf. = Felting bristles.
Sg. = Primary spermatogonium (others *f* and *g*).
Si. = Iridescent setae.
Sm. = Spermatozoon.
So. = Supporting cells of epithelium.
Som. = Superior oblique muscles.
Sp. = Dorsal spines.
Spc. = Spermatocyte.
Ss. = Setal sac.
St. = Spermatid.
Stg. = Stomato-gastric nerves.
Sv. = Setae of ventral row—neuropodium.

T. = Median tentacle.
TBm. = "Tags" of basement membrane.
Tub. = Dorsal tubercle (or elytrophore).

Uc. = Pear-shaped ganglion cell.

V. = Ventral edge of facial tubercle.
VG. = Ventral ganglion.
Vl. = Ventral lip of ciliated funnel.
Vm. = Ventral longitudinal muscles.
Vp. = Ventral plexus of blood vessels.
Vs. = Ventral sac.
Vv. = Ventral blood vessel.

Wt. = Cuticular wart.

Y. = Group of fibres passing from mid-lobule to posterior border of capsule.

I. = Excretory cells (of Darboux).
II. = Secretory cell (of Darboux).

Plate I.

Fig. 1*a*. Photograph of *A. aculeata*—dorsal surface.
Fig. 1*b*. *A. aculeata*—ventral surface view. Nat. size.
Fig. 2. Ventral view of anterior end of *A. aculeata*, pharynx protruded.
Fig. 2*a*. Posterior end of body—viewed from dorsal surface.

Plate II.

Fig. 3. Dorsal surface of anterior end, *A. aculeata*. × 10.
Fig. 4. Median tentacle—detached. × 40.
Fig. 5. Facial tubercle—lateral view. × 14.
Fig. 6. Posterior face of typical trunk parapodium of non-elytrous segment—from right side. × 4.
Fig. 7. Parapodium of Segment II—anterior face. × 10.
Fig. 8. Young neuropodial seta.
Fig. 9. Parapodium of Segment XLI—posterior face. × 16.

Plate III.

Fig. 10. Notopodial cirrus, typical. × 8.
Fig. 11. Dorsal fimbriated papillae from Segments VI (*a*). × 10, and XX (*b*). × 12.
Fig. 12. Nephridial papilla. × 20.
Fig. 13. Cuticle—surface view.
Fig. 14. Trans. sect. of ventral body wall. × 160.
Fig. 15. Portion of dorsal body wall stained to show peripheral nerves—from external surface. × 28.
Fig. 16. Supporting cells of epidermis. × 440.
Fig. 17. Trans. sect. epidermis at base of palp. × 650.
Fig. 18. Trans. sect. through wall of dorsal fimbriated papilla. × 125.

Fig. 19. Horizontal sect. through epidermis of figure 18. × 160.
Fig. 20. Columnar cells of epidermis—ventral body wall. × 360.
Fig. 21. Section through axis of spherical papilla of ventral body wall. × 260.
Fig. 22. Trans. sect. through integument of inferior lip. × 60.
Fig. 23. Section through axis of conical papilla of dorsal body wall. × 160.
Fig. 24. Longit. sect. of notocirrus. Diagram.
Fig. 25. Optical section of edge of cirrostyle to show sensory papillae. × 140.
Fig. 26. Sensory papilla of palp. × 600.

PLATE IV.

Fig. 27. Portion of trans. sect. of palp. × 160.
Fig. 28. Periphery of elytron—stained whole mount, dorsal surface view. × 415.
Fig. 29. Dissociated fibres from periphery elytron. × 350.
Fig. 30. Trans. sect. elytron near attachment area. × 250.
Fig. 31. Horizontal sect. of figure 30. × 180.
Fig. 32. General view of internal organs of mature female—the egg-bearing blood vessels are shown only on the left side of the drawing. Viewed from above. Nat. size.
Fig. 33. Coelomic epithelium—
  (*a*) Surface view (from prepared slide). × 1300.
  (*b*) Trans. sect. of ciliated patch. × 350.
Fig. 34. Three coelomic corpuscles (two fresh).
Fig. 35. *A. aculeata*, posterior end—ejection apparatus closed.
Fig. 36. *Hermione hystrix*, posterior end.
Fig. 37. Trans. sect. of "heart." × 630.

PLATE V.

Fig. 38. Diagrammatic trans. sect. body *A. aculeata*, to show principal blood vessels. (Adapted after Selenka.)

Fig. 39. Intestinal caecum from middle of body. × 3.

Fig. 40. Trans. sect. wall of buccal mass. × 120.

Fig. 41. Radial longit. sect. wall of pharynx. × 25.

Fig. 42. Single tuft of pharyngeal papillae. × 16.

Fig. 43. Trans. sect. through pharynx cutting bases of pharyngeal papillae (left dorsal quarter). × 6.

Fig. 44. Longit. sect. of a pharyngeal papilla. × 80.

Fig. 45. Trans. sect. through pharynx just anterior to tips of jaws (left dorsal quarter). × 6.

PLATE VI.

Fig. 46. Trans. sect. of pharyngeal papilla. × 300.

Fig. 47. Portion of epithelium, anterior region of pharynx.

Fig. 48. Trans. sect. through oesophagus towards posterior end. × 30.

Fig. 49. Portion of epithelium of figure 48. × 120.

Fig. 50. Longit. sect. junction of oesophagus and intestine. × 35.

Fig. 51. Trans. sect. of wall of intestine. × 130.

Fig. 52. Section through sieve (caecum). × 25.

Fig. 53. Single fresh cell of epithelium of sieve. × 90.

Fig. 54. Epithelium of caecum—one of the papillae. × 270.

PLATE VII.

Fig. 55. I to XI. Cells of caecal epithelium in detail. × 230. XII. Two *ballots d'excretion.*

Fig. 56. Trans. sect. of wall of rectum. × 130.

Fig. 57. Portion of blood vessel of mature female—with ripe ova. × 35.

Fig. 58. Portion of body cavity of female, showing groups of developing ova on blood vessels. Enlarged.

Fig. 59. Longit. sect. blood vessel, showing early stages of proliferation of sex cells—female. × 200.

Fig. 60. Longit. sect. blood vessel of maturing female with eggs of various ages. × 100.

Fig. 61 (*a* and *b*). Two sections of wall of "mature" blood vessel—male. × 330. (*c*) Four spermatids. (*d*) Spermatozoon.

Fig. 62. Trans. sect. wall of nephridium—excretory or yellow cells. × 800.

Fig. 63. Trans. sect. wall of nephridial funnel. × 360.

Fig. 64. Longit. sect. nephridial papilla. × 25.

PLATE VIII.

Fig. 65. Entire nephridium removed from right side of body—viewed from ventral surface.

Fig. 66. View looking into nephridial funnel—anterior aspect *in situ*.

Fig. 67. Muscles of typical body segment, left side, posterior aspect.

Fig. 68. Muscles moving neuropodia—ventral body wall. Left side viewed from coelom. Enlarged.

Fig. 69. Outer elytrophore muscles—dorsal body wall. Enlarged.

Fig. 70. A neuropodium opened along mid-ventral line, to show muscles and setae. Enlarged.

Fig. 71. Muscles at head of aciculum and setal sacs—neuropodium. Enlarged.

Fig. 72. Anterior portion of nervous system, showing first seven podial nerves.

Fig. 73. Diagram—stomato-gastric nervous system.

PLATE IX.

Fig. 74. Portion of palpary nucleus to show structure of nerve cells. × 360.

Fig. 75. Giant nerve cell. × 360.

Figs. 76-79. Four trans. sections through the prostomium from anterior to posterior end. Figs. 76-78 are from the same series. They are all slightly oblique so that the right-hand sides of the illustrations are somewhat anterior to the left. Fig. 79 is from a different series; it is transverse.

Fig. 76. Trans. sect. passing through the posterior part of the eyes. The right-hand side of the drawing shows the thickness of the neuroglia capsule and the anterior limit of the lateral coelomic canals (*L.coe.*). The left-hand side passes through the anterior end of the palpary nuclei (*Pg.*) and shows the separate anterior and mid-lobules. × 35.

Fig. 77. Trans. sect. posterior to the eyes, illustrating, on the right, the optic nerve and palpary nerve and the origins of the posterior ramus (*RP.*) and the stomato-gastric nerves (*RS.*). On the left these two latter pass beneath the palp. × 35.

Fig. 78. Trans. sect., the right side of which is just posterior to the left side of figure 77. It illustrates the origins of the optic nerves. On the right-hand side it is similar to figure 77 (left). The left-hand side illustrates the passage of the fibre " stalk " of the palpary nuclei into the anterior lobule—and the double origin of the anterior rami (*RA.*) from this region and from the palpary nuclei. × 35.

PLATE X.

Fig. 79. Trans. sect. somewhat posterior to figure 78. It passes through the posterior part of the prostomial coelom (*P.coe.*). The central mass of ganglion cells belongs to the mid-lobule. × 50.

Figs. 80-82. Three sagittal sections of the prostomium from the median plane to the right-hand side. (From different series of sections.)

Fig. 80. Median longit. sect. through the prostomium. It illustrates the passage of the coelom (*P.coe.*) into the median coelomic canal (*M.coe.*) and the extension of the latter into the median tentacle. The central fibres mass is not divided into the mid and anterior lobules. × 55.

Fig. 81. Longit. sect. just within the base of the right palp, illustrating the optic nerves, posterior ramus and stomato-gastric ramus. × 55.

Fig. 82. Longit. sect. through the outer side of the base of the palp. The anterior and dorsal region (passing through the eye) lies nearer the axial plane than the diagonally opposite border of the section. The section therefore illustrates both the anterior ramus (*RA.*) and the palpary nerve (*PpN.*). × 55.

Fig. 83. Pear-shaped ganglion cells of the anterior lobule with surrounding neuroglia. × 350.

Fig. 84. Trans. sect. sub-oesophageal ganglion. × 40.

Fig. 85. Trans. sect. ventral ganglion. × 50.

Fig. 86. Trans. sect. through posterior part of one of the oesophageal commissures. × 70.

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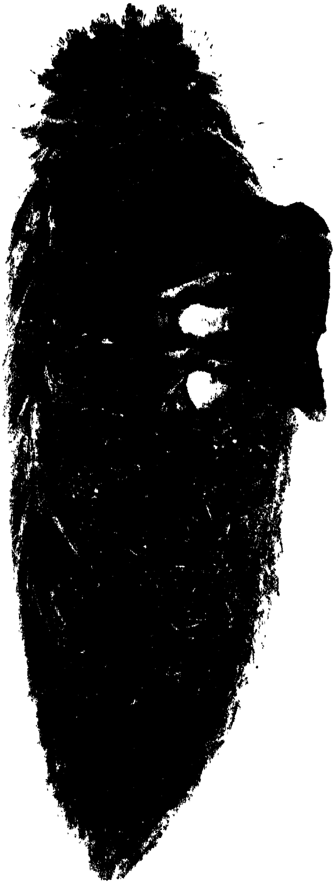

FIG. 1*a*

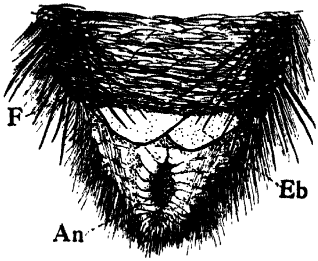

FIG. 2*a*

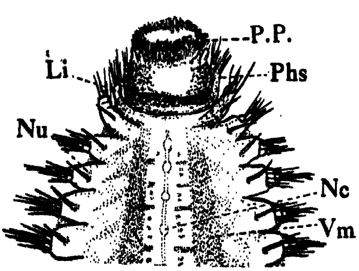

FIG. 2

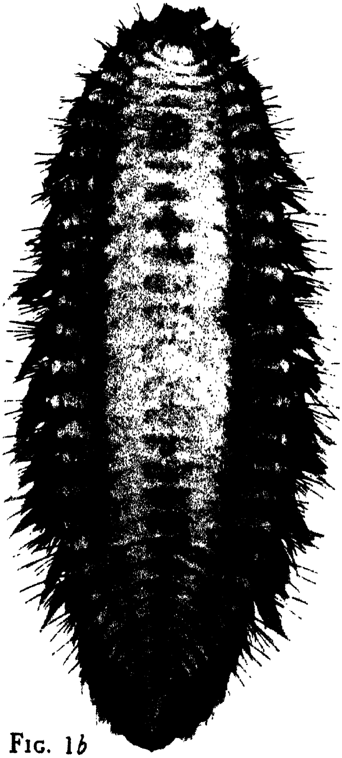

FIG. 1*b*

APHRODITE ACULEATA

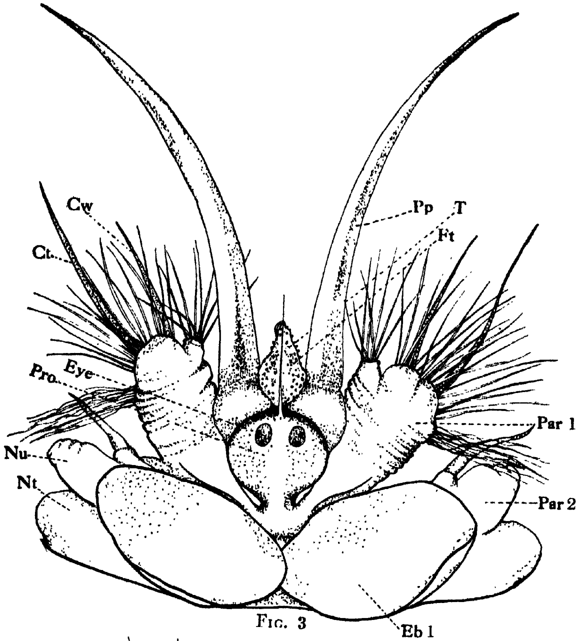

FIG. 3

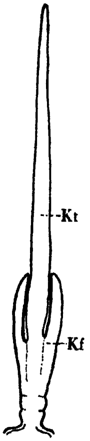

FIG. 4

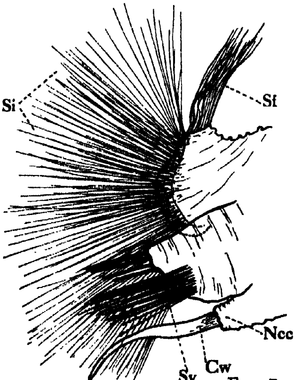

FIG. 7

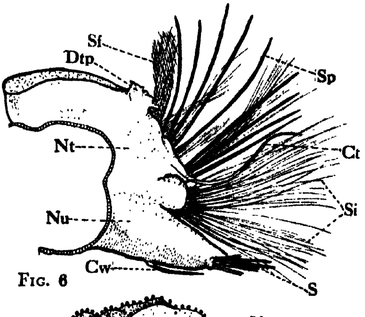

FIG. 6

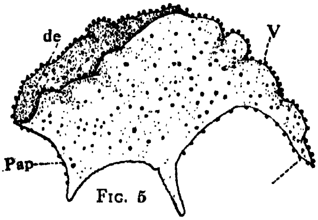

FIG. 5

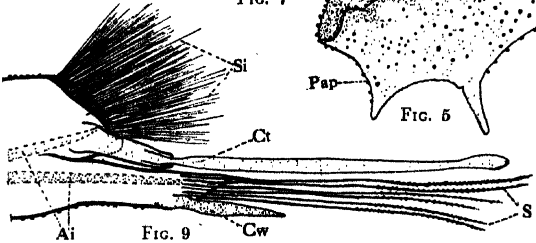

FIG. 9

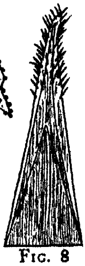

FIG. 8

APHRODITE ACULEATA

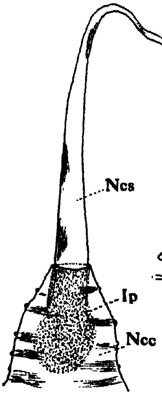

Fig. 10

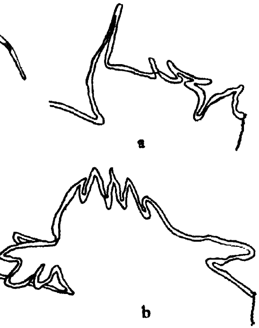

Fig. 11

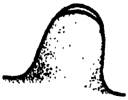

Fig. 12

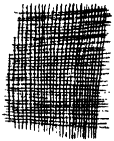

Fig. 13

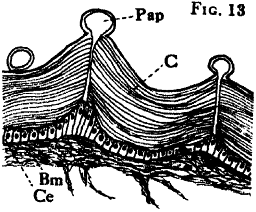

Fig. 14

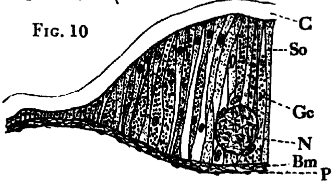

Fig. 18

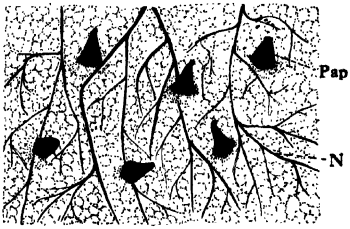

Fig. 15

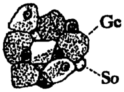

Fig. 19

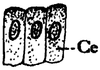

Fig. 20

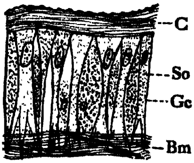

Fig. 17

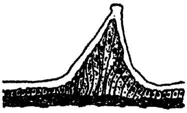

Fig. 23

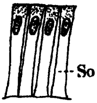

Fig. 16

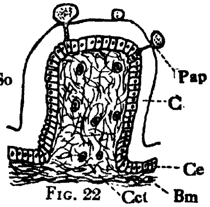

Fig. 22

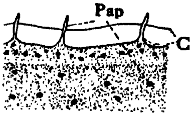

Fig. 25

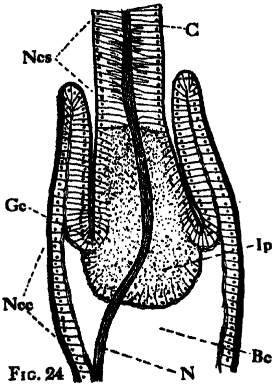

Fig. 24

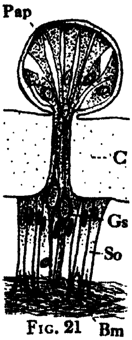

Fig. 21

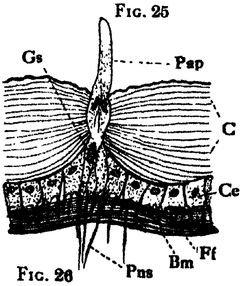

Fig. 26

APHRODITE ACULEATA

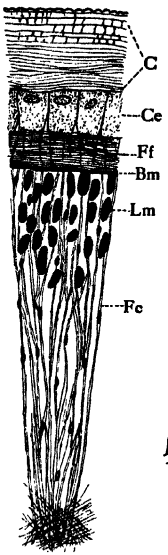

FIG. 27

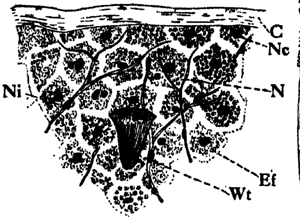

FIG. 28

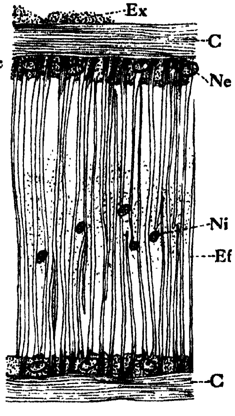

FIG. 30

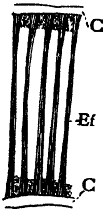

FIG. 29

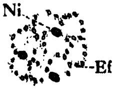

FIG. 31

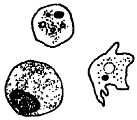

FIG. 34

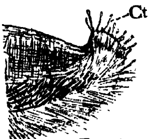

FIG. 35

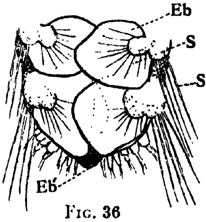

FIG. 36

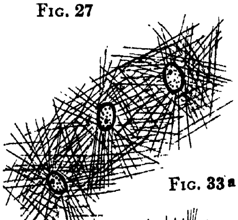

FIG. 33 a

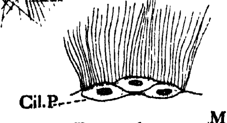

FIG. 33 b

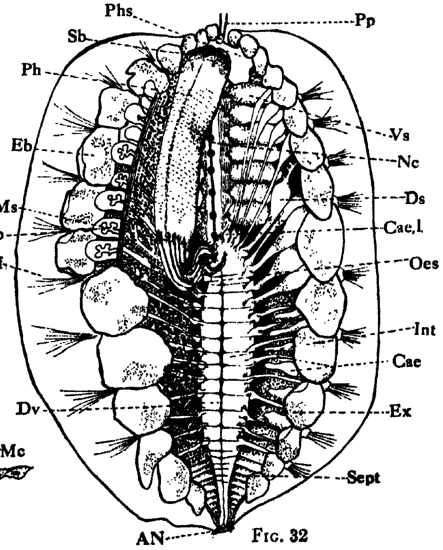

FIG. 32

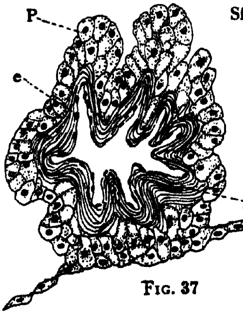

FIG. 37

APHRODITE ACULEATA

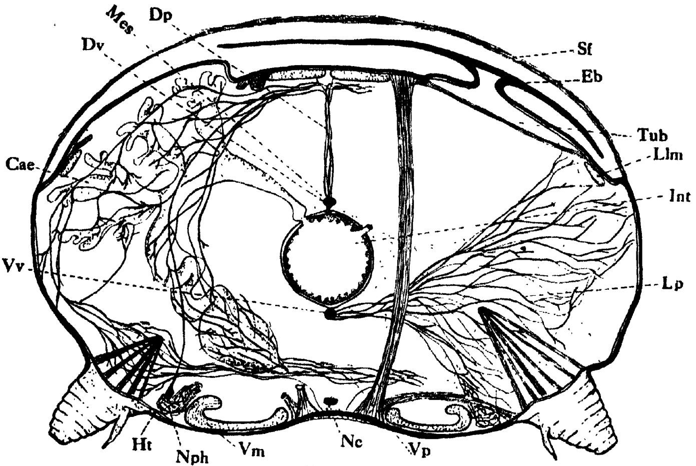

FIG. 38

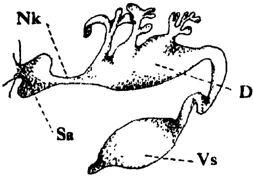

FIG. 39

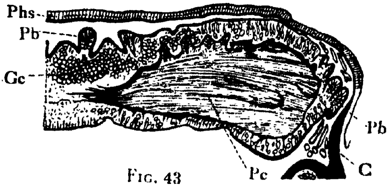

FIG. 43

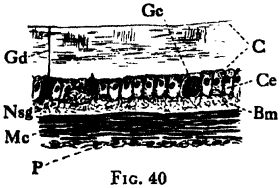

FIG. 40

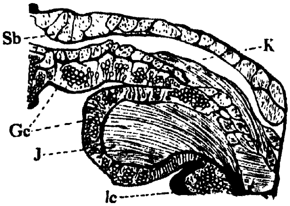

FIG. 45

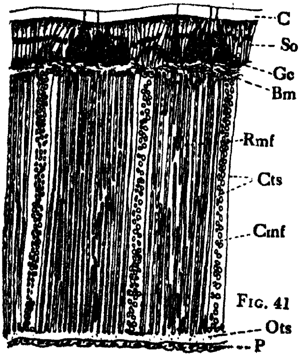

FIG. 41

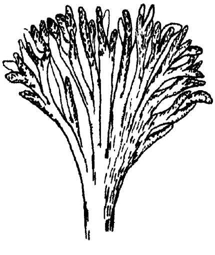

FIG. 42

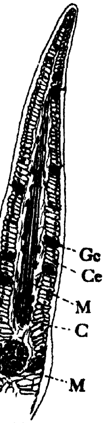

FIG. 44.

APHRODITE ACULEATA

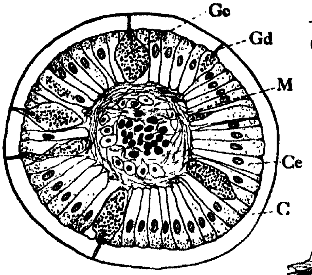

Fig. 46

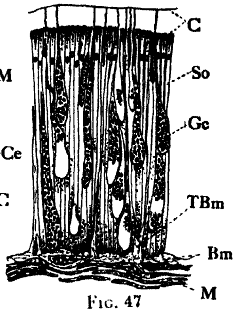

Fig. 47

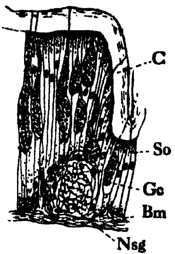

Fig. 49

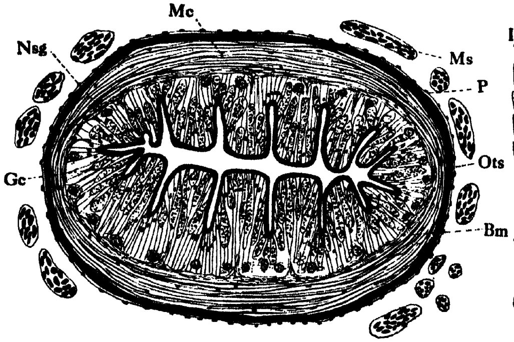

Fig. 48

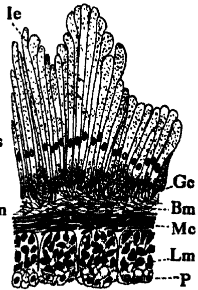

Fig. 51

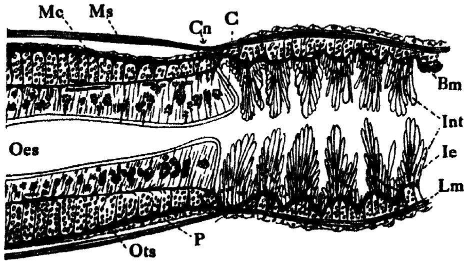

Fig. 50

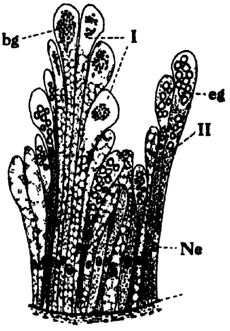

Fig. 54

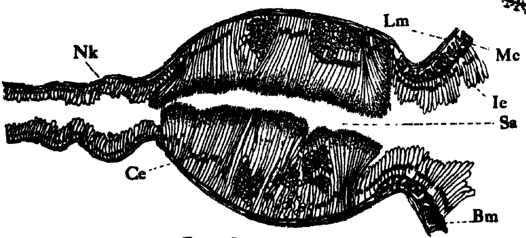

Fig. 52

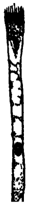

Fig. 53

APHRODITE ACULEATA

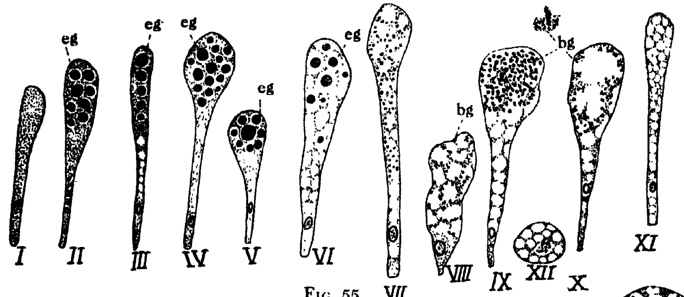

FIG. 55

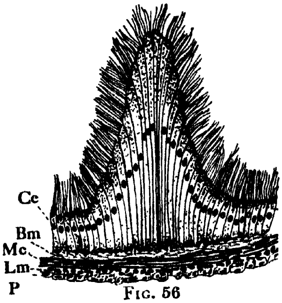

FIG. 56

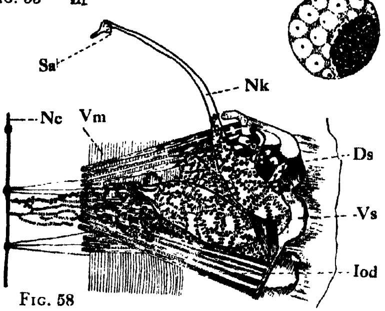

FIG. 58

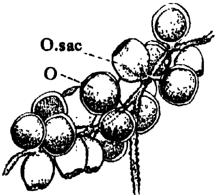

FIG. 57

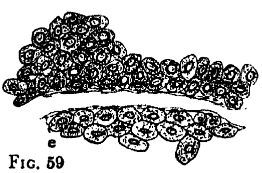

FIG. 59

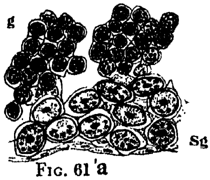

FIG. 61 a

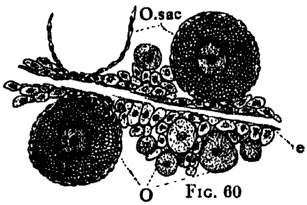

FIG. 60

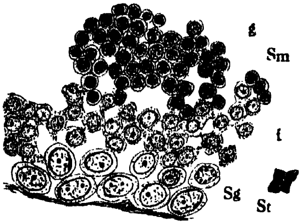

FIG. 61 b

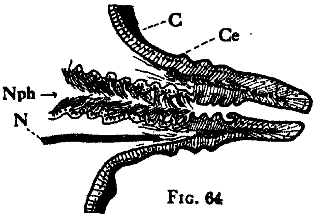

FIG. 64

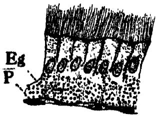

FIG. 62

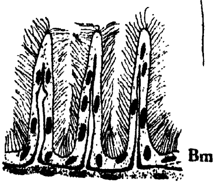

FIG. 62

APHRODITE ACULEATA

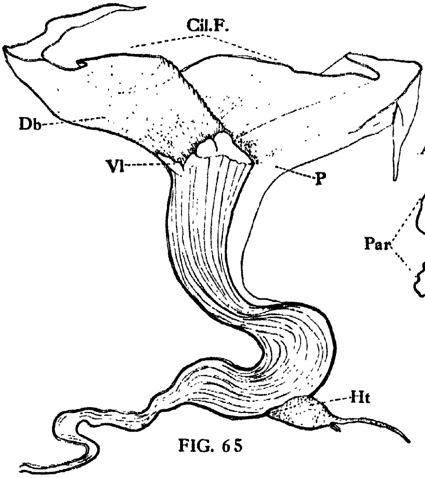

FIG. 65

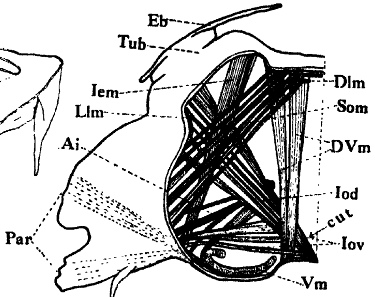

FIG. 67

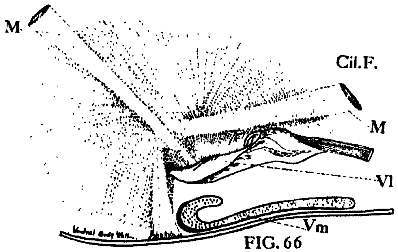

FIG. 66

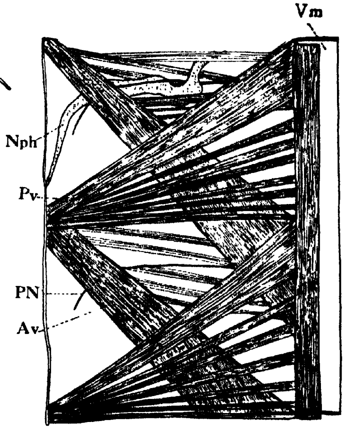

FIG. 68

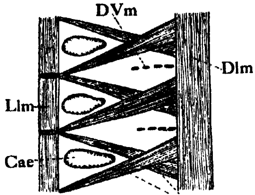

FIG. 69

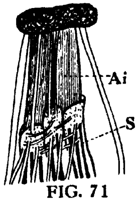

FIG. 71

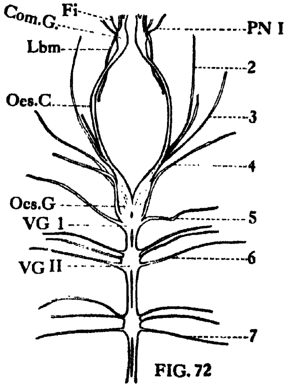

FIG. 72

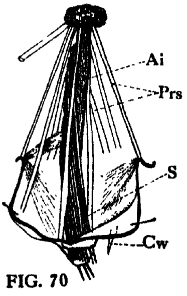

FIG. 70

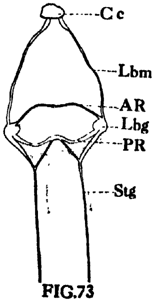

FIG.73

APHRODITE ACULEATA

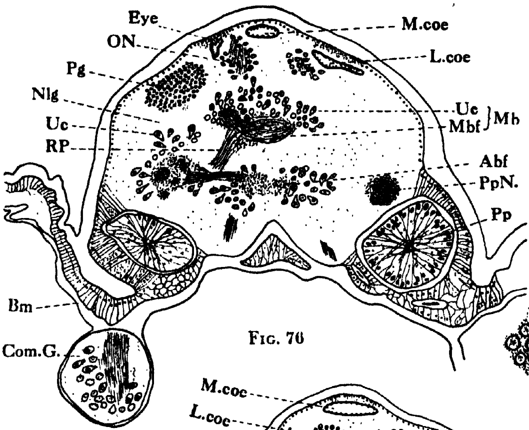

FIG. 76

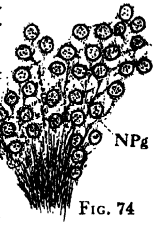

FIG. 74

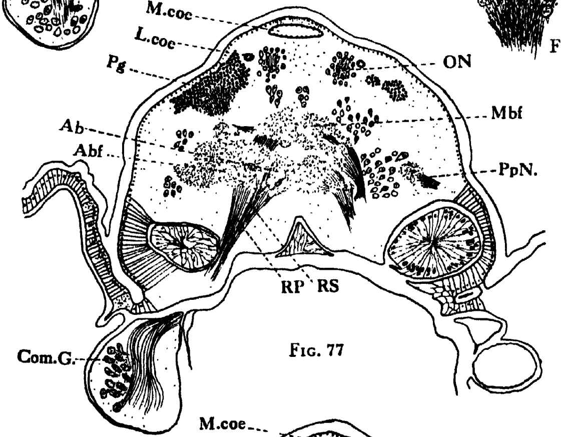

FIG. 77

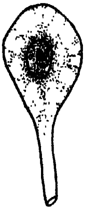

FIG. 75

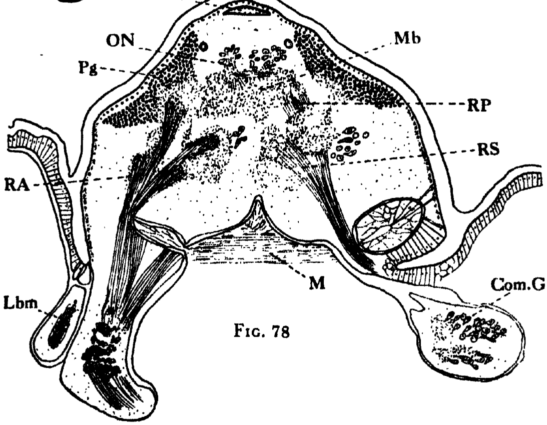

FIG. 78

APHRODITE ACULEATA

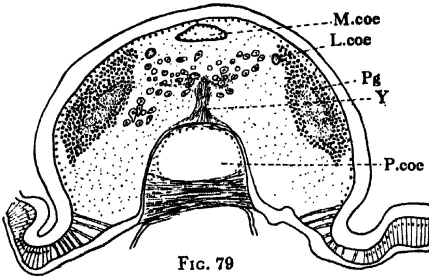

Fig. 79

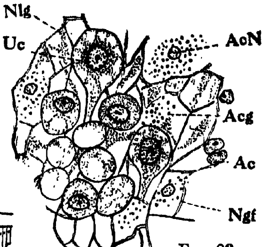

Fig. 83

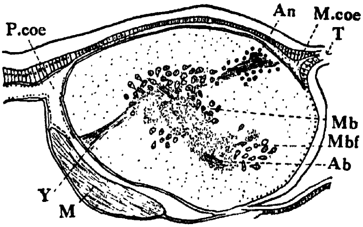

Fig. 80

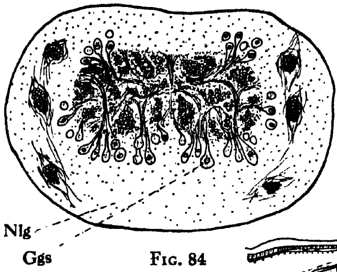

Fig. 84

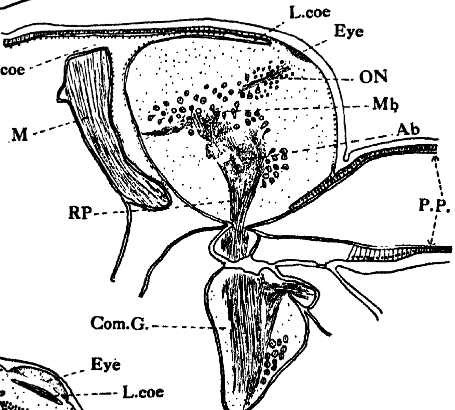

Fig. 81

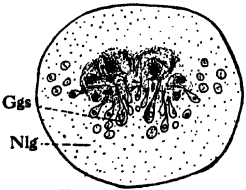

Fig. 85

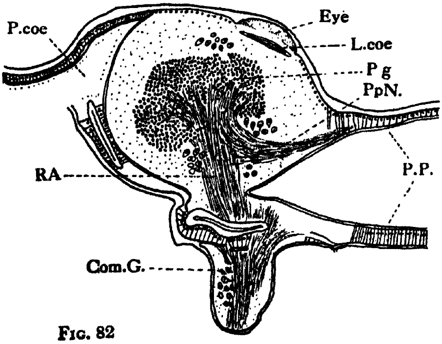

Fig. 82

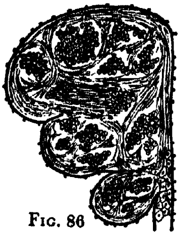

Fig. 86

APHRODITE ACULEATA